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Vegetative Anatomy of the Hawaiian Species of *Santalum* (Santalaceae)[1]

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ABSTRACT: Wood and foliar anatomy of the Hawaiian representatives of the genus *Santalum* are described. No consistent differences in wood anatomy between taxa were found; however, significant anatomical differences in foliar anatomy were observed. Characteristics of leaf anatomy that are of taxonomic value are the bottle-shaped adaxial epidermal cells of *S. haleakalae*, the papillate nature of the abaxial leaf surface in several taxa, and the presence of adaxial as well as abaxial stomata in *S. ellipticum*.

SEVEN SPECIES OF *Santalum* from Hawai'i have been recognized in the past. Nomenclature in this paper follows the recent revision of the genus (Stemmermann 1980). The sandalwoods are separated into two groups generally thought to be derived from separate introductions to Hawai'i (Rock 1916, Skottsberg 1927, 1930, Tuyama 1939, Fosberg 1948). The *freycinetianum* group (including *S. haleakalae*, *S. freycinetianum*,[3] *S. freycinetianum* var. *lanaiense*, *S. freycinetianum* var. *auwahiense*, and *S. freycinetianum* var. *pyrularium*) is characterized by having flowers that are usually reddish, with long perigonal tubes. The *ellipticum* group (including *S. ellipticum*, *S. ellipticum* var. *littorale*, *S. paniculatum*,[3] and *S. paniculatum* var. *pilgeri*) is characterized by having flowers that are greenish at anthesis, with short, perigonal tubes. Some, perhaps all, of the species were harvested during the sandalwood trade in the nineteenth century, and formed one of the first bases of commerce for the Kingdom of Hawai'i after European contact.

The taxa of the Hawaiian sandalwoods have been distinguished by previous authors on gross characteristics of the flowers, fruit, leaves, and growth habits of the plants, but until now no complete anatomical study of the wood of the various taxa has been made. Though the wood of at least three Hawaiian taxa, probably *S. paniculatum* var. *pilgeri*, *S. freycinetianum*, and *S. freycinetianum* var. *pyrularium*, has been examined in previous studies (Brown 1922, Metcalfe 1935), it is impossible to be certain which taxa were actually investigated due to confusion of the original diagnoses of *S. freycinetianum* and *S. ellipticum*. Furthermore, at least four taxa were not examined at all. Therefore, since the wood of the genus *Santalum* has been significantly important in the economy of Hawai'i, and review of the literature demonstrated a paucity of information on the wood anatomy of the Hawaiian taxa, a study was undertaken to determine whether any differences in the wood exist among the species or sections of the genus *Santalum* in Hawai'i.

In addition, though gross foliar features have been used to distinguish among the Hawaiian taxa of *Santalum* (Skottsberg 1927, Degener 1940), no anatomical descriptions or comparisons of the leaves of the taxa had been made. This study therefore also examined foliar anatomy of all the taxa to determine the anatomical basis for characters of apparent taxonomic significance.

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[3] For *S. freycinetianum*, *S. ellipticum*, and *S. paniculatum*, the typical variety is assumed unless another is specifically mentioned.

MATERIALS AND METHODS

Fresh wood samples were collected from populations of each of the recognized species of *Santalum*. Voucher herbarium specimens were prepared for each sample and were deposited in the herbarium at the University of Hawaii (HAW). Wood samples were taken from branches ranging from 5 (rarely 4) to 9 cm in diameter, fixed in Craf III, and aspirated to allow for rapid fixation of the tissues. After at least a week of fixation the samples were transferred to alcohol and sectioned on a sliding microtome. Sections were stained in tannic acid–ferric chloride–lacmoid according to Cheadle, Gifford, and Esau (1953) and mounted in synthetic resin.

Macerations were prepared by placing slivers of wood in a solution of 1 part 30 percent hydrogen peroxide, 4 parts water, and 5 parts glacial acetic acid (Gifford et al. 1956). Macerating fluid was changed at 3-day intervals until the maceration process was complete, usually after about 5 days. Material was then rinsed, stained with a tannic acid mordant followed by ferric chloride and safranin O, dehydrated in an ethanol series to xylene, and mounted in synthetic resin.

The wood morphology of *Santalum ellipticum* var. *littorale* was not studied for several reasons. That taxon is on proposed lists of endangered species for Hawai'i (Fosberg and Herbst 1975, U. S. Department of the Interior 1976), and as the plant is a low shrub, with no sizable branches except for the central axis of the plant, most of an entire plant would have had to be taken to do an analysis that could be comparable with the other taxa examined. Since analysis of wood morphology of the other taxa showed no consistent differences of taxonomic significance; because the habit of the plant is such that the wood could not be of economic importance; and since it is found in semiarid conditions where regrowth is slow, it was felt that any information gathered on its wood morphology would not be of sufficient interest to warrant the taking of a plant.

Leaf samples were collected from the same populations as the wood samples and fixed in Craf III, with aspiration when possible. Leaves to be sectioned were dehydrated in an ethanol tertiary butanol series, infiltrated with Parowax, finally embedded in Paraplast, and sectioned on a rotary microtome. Cross sections and paradermal sections were cut through the widest part of the lamina and perpendicular to the midrib. The sections were mounted and then stained in Johansen's quadruple stain (Johansen 1940), toluidine blue O (Sakai 1973), or various schedules of tannic acid–ferric chloride, safranin O, and fast green.

Leaf clearings were prepared by placing fixed leaves in the paraffin oven in a solution of 50 g chloral hydrate, 25 ml liquid phenol, and 35 ml lactic acid, until clearing was complete. The cleared leaves were rehydrated and stained with tannic acid–ferric chloride and safranin O or safranin and celestine blue (Gray and Pickle 1956), dehydrated, and mounted in resin.

To determine silica body integrity and shape, a few macerations of leaves were prepared using the same solution and staining technique used for wood maceration. In addition to this, the percent weight of silica bodies in leaves of a few samples was determined by recording the dry weight of leaves, ashing them in a muffle furnace in porcelain crucibles, reweighing them, and recording the ashed weight. The ash was treated with approximately 10 percent concentrated H_2SO_4, 90 percent concentrated HNO_3, and a few drops of 30 percent H_2O_2. The treated ash was then left on a hot plate for a week until the carbon had been removed, and the remaining substance was filtered on ashless filter paper, re-ashed, and reweighed.

Basic statistics for wood morphology were based on 20 measurements per sample for some attributes: extreme vessel body length, fiber length, vessel diameter, ray height, and vessel distribution. Ten measurements per sample were made for the other examined wood characteristics and for most foliar characteristics examined.[4]

[4] Refer to M.S. thesis deposited at the University of Hawaii for actual numerical analyses (Stemmermann 1977).

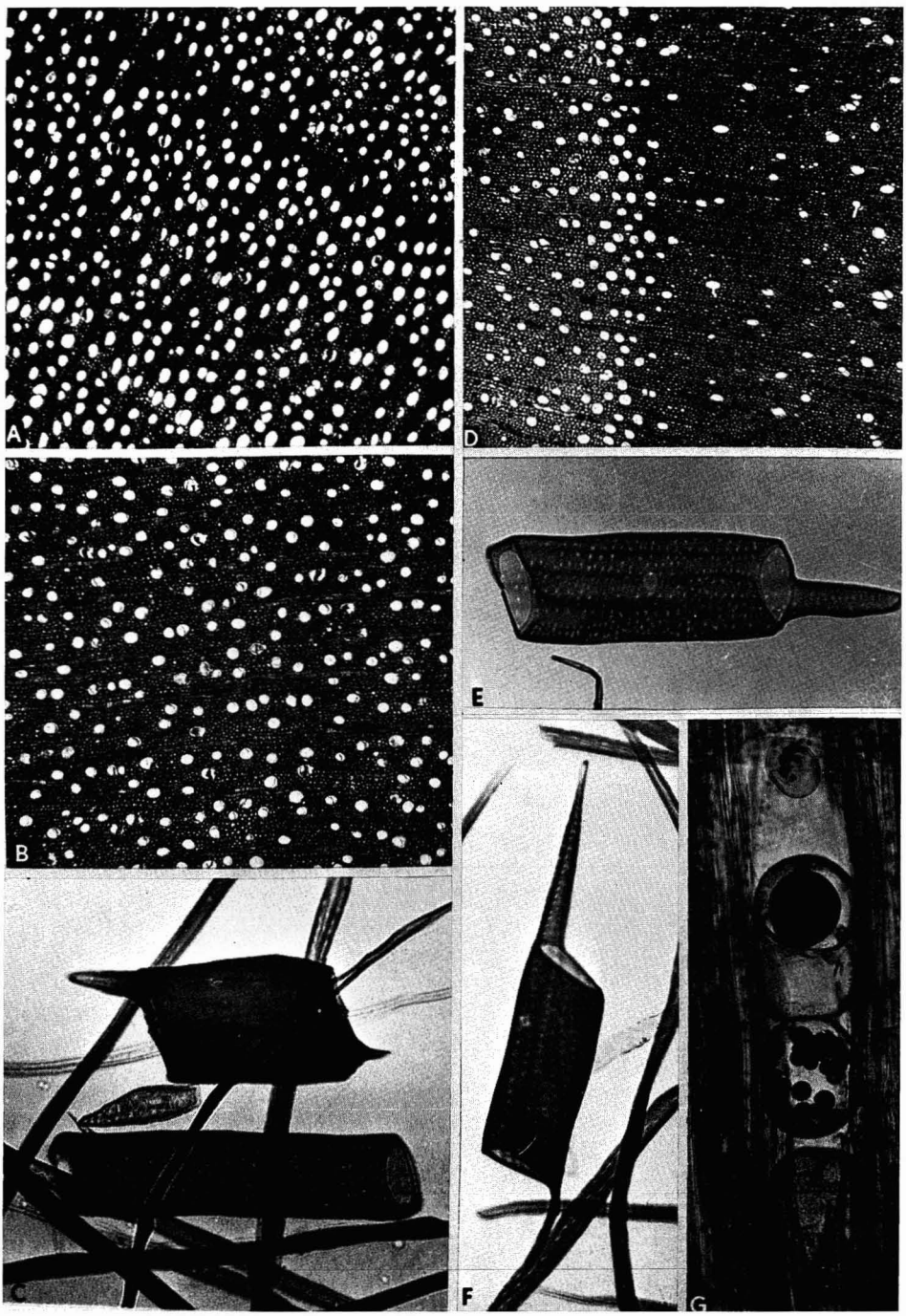

FIGURE 1. Wood morphology—vessel characteristics of Hawaiian *Santalum*. *A*, semi-ring porous arrangement of vessels in *S. haleakalae* (*L. Stemmermann* 737) ×29; *B*, diffuse porous arrangement of vessels in *S. haleakalae* (*L. Stemmermann* 750) ×29; *C*, tailed and transverse to slightly oblique vessel end walls in one sample of *S. paniculatum* (*L. Stemmermann* 799) ×177; *D*, ring porous arrangement of vessels in a sample of *S. paniculatum* var. *pilgeri* (*Pat Conant* s.n.) ×29; *E*, single-tailed vessel member of *S. paniculatum* (*L. Stemmermann* 799) notice circular structure in the side wall as discussed in the text ×177; *F*, double-tailed vessel member of *S. paniculatum* (*L. Stemmermann* 791B) with circular structure in side wall ×177; *G*, tyloses with resinous contents in vessel of *S. freycinetianum* (*L. Stemmermann* 801) ×177.

RESULTS

Wood

GROSS MORPHOLOGY: The sapwood of all the examined species of *Santalum* is yellowish in color, while the heartwood becomes brown, sometimes with a reddish hue. Only the heartwood is aromatic, and in samples taken for this research from branches less than 9 cm in diameter, little or no heartwood had developed.

The wood of all the examined species of *Santalum* is diffuse porous (Figure 1*B*) or sometimes tending toward ring porous (Figure 1*A*, *D*). Occasionally, rings are found in the wood where vessels are either absent or very abundant, but the tendency of the wood to show either of these patterns is not a taxonomically useful criterion. Rings have also been seen in *S. album*, and at least in that taxon it was demonstrated that these should not be considered annual rings (Troup 1919, Chowdhury and Ghosh 1950).

Standardized descriptive terminology is used in discussion of the various cellular and structural components of the secondary xylem (Chattaway 1932, Chalk and Chattaway 1934, Committee on Standardization of Terms of Cell Size 1937, 1939, Committee on Nomenclature 1957).

VESSELS: The length of vessels in *Santalum* is generally greater than their width (Figure 1*C*, *E*, *F*). Their end walls are usually oblique with tapering tails, though transverse end walls are not uncommon, and both tailed and tailless vessels can be observed in all samples (Figure 1*C*, *E*, *F*). Only simple perforations are present.

Discussion of vessel length is based on the measurement of the extreme body length in macerations. The vessels were found to be short to medium sized, ranging from 91 to 379 μm. Though measurement of extreme body length of vessels has been advocated (Chattaway 1932), the measurement of total member length has generally been preferred (Chalk and Chattaway 1934, 1935, Carlquist 1961). Therefore, the length of vessels was also analyzed using this measurement. Based on that analysis, the vessels were again found to be short to medium sized, ranging from 141 to 576 μm. These data are in agreement with previous reports for vessel lengths for Santalacean species (Swamy 1949) and for *S. freycinetianum* var. *pyrularium* (Brown 1922).

Both radial and tangential vessel diameters were measured, and vessels were found to be round to oval and to range from being very small to small, or rarely extremely small or moderate sized. Radial diameters range from 31 to 113 μm, and tangential diameters range from 22 to 56 μm.

Vessel walls are about the same thickness in all the examined taxa, ranging from 1.2 to 3.6 μm thick and averaging 2.7 μm. The side walls of the vessel members have alternate circular bordered pits with lenticular apertures, and these were sometimes arranged in vertical rows. In maceration, vessels were frequently seen to have one or more structures on their side walls that resembled lateral perforations (Figure 1*E*, *F*). Whether such structures occurred between vessel members or between a vessel member and a parenchyma cell could not be determined, as there is some evidence for both.

The general appearance of these structures gives the impression that they might be perforations, or possibly intervascular pits, but since vessels occur singly in *Santalum* with very few exceptions, the second explanation is ruled out. Conceivably, such structures could occur between the tail of one vessel and the body of another, in which case these structures could properly be called perforations. Even though such structures have been observed on both vessel bodies and tails, they usually occur on the vessel body rather than on the tail, and no preparations were observed that demonstrated tail to body pairing had occurred.

In maceration, occasionally one of these structures in the vessel wall is observed next to a parenchyma cell, but whether such juxtaposition is an artifact of the maceration process was not determined. There are quite large circular pits on the walls of both axial parenchyma and radial parenchyma cells, but the diameter of the pits is less than the

diameter of cells. Thus, if the two areas are normally associated, the pairing is imperfect. Solereder (1908) includes the Santalaceae in his list of families where "simple and occasionally large pits on the walls of the vessels" occur in contact with parenchyma, and this is probably how he interpreted these structures. I favor this explanation. Other authors (Brown 1922, Metcalfe and Chalk 1950) do not discuss these structures.

The average number of vessels per square millimeter was calculated from counts of 20 microscope fields of 0.292 mm^2. The distinction between fiber tracheids and vessels is obscure in some samples and could not be made in transverse section, so no element was counted if its radial diameter was less than 10 units on the ocular micrometer (approximately 31 μm). It was necessary to make this arbitrary decision in only a very few samples. Since none of the means or variances of vessel diameter measurements approach this value, this sampling technique probably did not produce biased data. Samples that were semi-ring porous exhibited high standard deviations, standard errors, and ranges, as would be expected; and those samples with the highest calculated variance tended toward ring porosity. Since in some samples within a taxon there was no overlap in the range of the number of vessels per square millimeter, basic statistics were determined for individual samples as well as for each taxon. The number of vessels per square millimeter varied considerably among samples within a taxon and within a given sample (as in samples displaying ring porosity), and therefore variations among taxa were often no larger than variations within a single taxon. The number of vessels per square millimeter ranged from an average of 30 in *Santalum freycinetianum* to an average of 68 in *S. haleakalae*.

Though Metcalfe and Chalk (1950) report that tyloses are usually present in the family, Brown (1922) specifically reported the absence of tyloses in *Santalum pyrularium* and made no mention of them in the other species he sampled. In this study tyloses were observed in the older vessels of all taxa examined, including *S. freycinetianum* var. *pyrularium*, and these tyloses often contain dark-staining resinous compounds or tannins, as do both radial and axial parenchyma surrounding the vessels (Figure 1*G*).

FIBER TRACHEIDS: The fiber tracheids of *Santalum* are very short to short, ranging from 480 to 1380 μm. Chattaway (1932) suggests that classes of fiber tracheid wall thickness be based on the comparison of the lumen diameter to the thickness of the walls separating one lumen from the lumen in the next cell. No constant pattern was observed, as both thick-walled and thin-walled samples were observed in each taxon, and usually both conditions were present in each sample. The lumen diameter ranged from 2.4 to 13.2 μm. Wall thickness ranged from 1.8 to 6 μm. Fiber walls have one to four rows of bordered pits with crossed lenticular apertures (Figure 2*A*). Ergastic inclusions were absent from fibers.

RADIAL PARENCHYMA: Both uniseriate rays and multiseriate rays are present in the wood of *Santalum*, with most of the multiseriate rays being biseriate (Figure 2*B*, *E*). Upright, square, and procumbent cells are present in all taxa (Figure 2*C*), with the biseriate rays generally having only uniseriate tails one cell high of upright cells. Simple circular pits occur on the walls of the radial parenchyma, and these are often obscured by the presence of dark-staining inclusions that are probably tannins (Figure 2*D*). Crystalliferous chains of axial parenchyma often seem to be associated with rays, but no crystals were ever seen in the ray cells. The number of rays per millimeter was determined by counting the number of rays intersecting a 1-mm line perpendicular to the vertical axis of a tangential section. They were found to be moderately numerous, ranging from 1 to 14 rays/mm.

The height of multiseriate rays was measured both in terms of cells and in terms of microns. Rays were found to be very low to rather low, or rarely moderately high, ranging from 71 to 811 μm, and from 3 to 25 cells high. Since most of the multiseriate rays are in fact biseriate in the genus *Santalum*, widths were measured only of biseriate rays so that differences between taxa would be

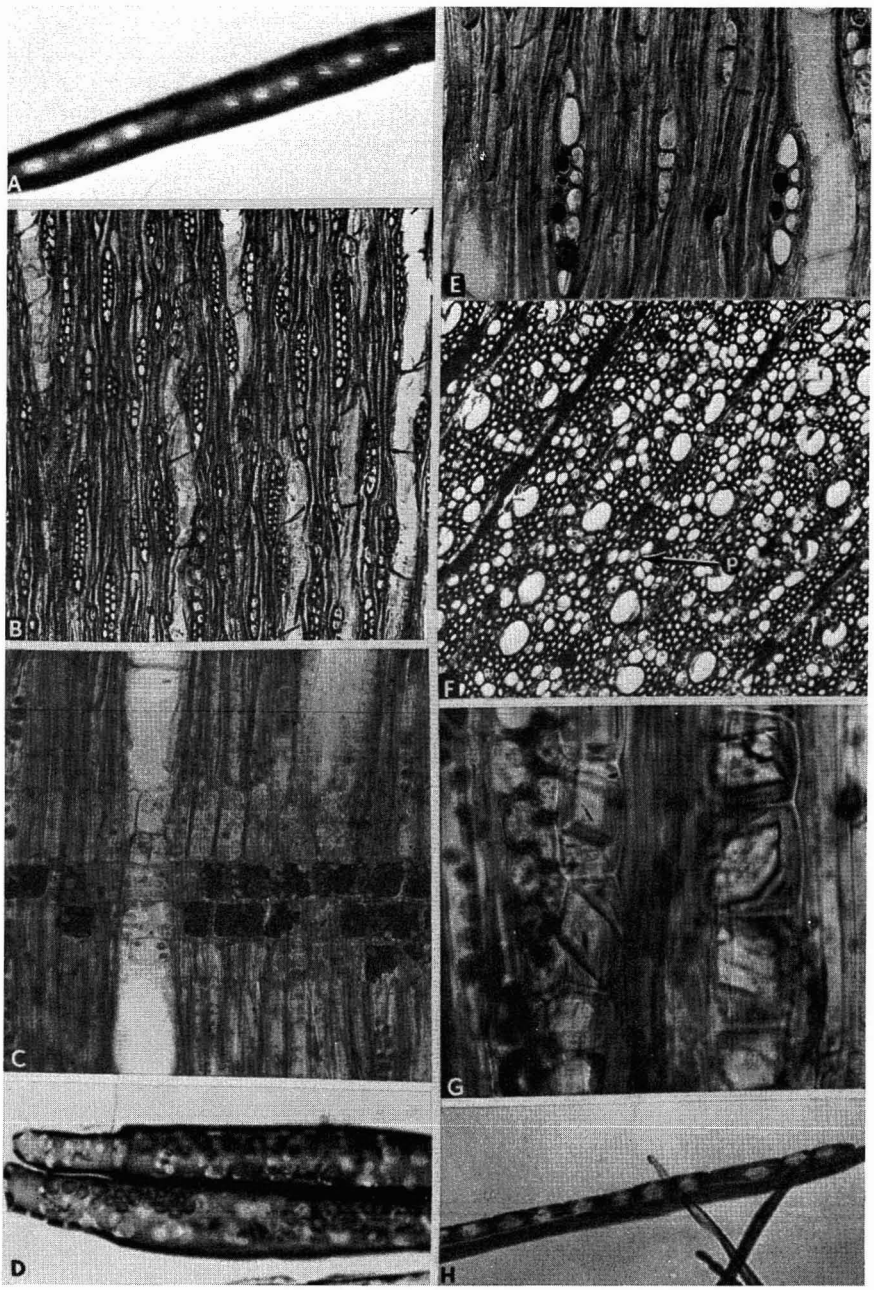

FIGURE 2. Wood morphology—fiber and parenchyma characteristics of Hawaiian *Santalum*. *A*, pits with lenticular apertures in fiber wall of *S. paniculatum* var. *pilgeri* (*P. Conant* s.n.) ×425; *B*, tangential section of *S. paniculatum* (*L. Stemmermann* 799) showing uniseriate and biseriate rays ×65; *C*, radial section of *S. freycinetianum* var. *pyrularium* (*L. Stemmermann* 786) demonstrating square, procumbent and upright ray cells ×168; *D*, axial parenchymal cells of *S. paniculatum* var. *pilgeri* (*P. Conant* s.n.) in maceration—notice tanniniferous contents and large simple circular pits ×425; *E*, uniseriate and biseriate rays in *S. ellipticum* (*L. Stemmermann* 761) ×168; *F*, diffuse in aggregate parenchyma in transection of *S. haleakalae* (*L. Stemmermann* 739) p = parenchyma cell, ×65; *G*, tangential section showing crystalliferous axial parenchyma of *S. ellipticum* (*L. Stemmermann* 781) ×425; *H*, crystalliferous axial parenchyma in maceration of *S. paniculatum* (*L. Stemmermann* 791B) ×168.

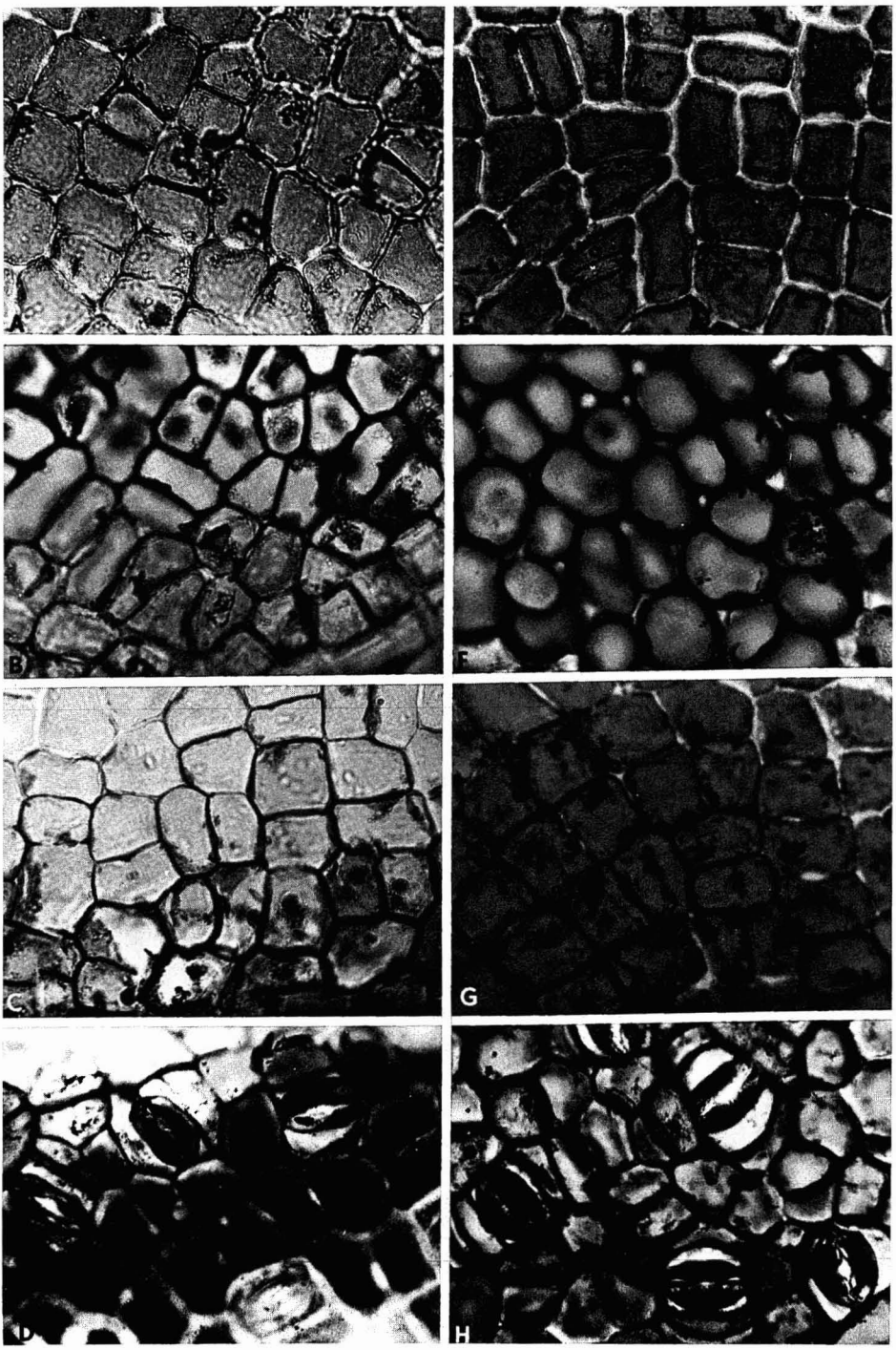

FIGURE 3. Paradermal sections of adaxial foliar epidermis of Hawaiian *Santalum*. Notice the pairs of rectangular cells that are oriented perpendicular to each other. Only *S. ellipticum* (*D*) and *S. ellipticum* var. *littorale* (*H*) have stomata in the adaxial epidermis. All ×450. *A*, *S. freycinetianum* (O'ahu) (*L. Stemmermann* 632); *B*, *S. freycinetianum* var. *auwahiense* (*L. Stemmermann* 575); *C*, *S. paniculatum* (*L. Stemmermann* 666); *D*, *S. ellipticum* (*L. Stemmermann* 746); *E*, *S. freycinetianum* var. *pyrularium* (*L. Stemmermann* 777); *F*, *S. haleakalae* (*L. Stemmermann* 750); *G*, *S. paniculatum* var. *pilgeri* (*L. Stemmermann* 679B); *H*, *S. ellipticum* var. *littorale* (*L. Stemmermann* 628).

based on truly comparable samples, and the variances within a sample would reflect that of the size of the ray cells rather than the number of cells in a ray. Biseriate rays were found to be very fine, their widths ranging from 14 to 47 μm in tangential section.

The height of uniseriate rays was also measured in terms of cells and microns. They were found to range from extremely low to rather low, ranging in height from 24 to 235 μm and consisting of from one to six cells. Uniseriate rays were extremely to very fine; their width ranged from 2.9 to 23.7 μm.

AXIAL PARENCHYMA: The length of axial parenchyma cells is generally several times greater than their diameter, though shorter cells exist. The axial parenchyma is apotracheal diffuse to diffuse in aggregate (Figure 2*F*), but no consistent differences were seen among taxa. Fairly large circular pits were found on the walls of the cells (Figure 2*D*). Chains of crystalliferous parenchyma are seen in longitudinal sections of all taxa (Figure 2*G*, *H*). These cells are shorter than the noncrystalliferous parenchyma, indicating either that the cells were smaller originally, or that the longer parenchyma cells subdivided preceding or following crystal formation, as has been suggested by Chattaway (1956). These chains do not easily dissociate in maceration (Figure 2*H*), which could be evidence for the initial deposition of the crystals in the longer axial parenchyma cells. The crystals are generally rhomboidal in shape, and rarely is there more than one crystal in a given cell. In addition to crystalliferous axial parenchyma, many parenchyma cells—especially in the older wood, but sometimes throughout a sample—contain dark-staining amorphous contents that are probably tannins.

Leaves

GROSS MORPHOLOGY: Leaves in the Hawaiian species of *Santalum* are opposite, and may be either petiolate or sessile. Leaf texture may be chartaceous, coriaceous, or succulent, and leaf thickness varies accordingly. Because certain taxa occur in more than one ecological zone, a range of environmental influences affects foliar development. This accounts for the large variation observed in leaf thickness for all taxa. *Santalum ellipticum* var. *littorale* has exceptionally thick leaves; the oldest leaves on a plant in some instances exceed 2 mm in thickness. But other taxa cannot be separated from each other on the basis of leaf thickness. Discussion of individual tissues in the leaf, and other characteristics of the foliar morphology follows using standard descriptive terminology (Carlquist 1961, Esau 1965, Fahn 1964).

ADAXIAL EPIDERMIS: The adaxial epidermal cells are rectangular to polygonal in shape, as viewed in either leaf clearings or paradermal sections (Figure 3). Pairs of rectangular cells that apparently arise from the same isodiametric mother cell are often present. The width of the cells is usually greater than or equal to the height of the cells. However, in *Santalum haleakalae* (*sensu stricto*, excluding lower-elevation plants from Maui), the adaxial epidermal cells are higher than wide and are of a peculiar bottle shape (Figure 4*F*). Furthermore, the diameter of the cells in that taxon is not as great as that of the other taxa (Figure 3). The development of this cell type is apparently correlated with some environmental factor associated with high elevations, such as ultraviolet radiation or low temperature, since a linear relationship can be demonstrated between the height of the adaxial epidermal cells of the *freycinetianum* group sandalwoods from Haleakalā and elevation (Figure 5).

Stomata are normally present in the adaxial epidermis in addition to the abaxial epidermis only in *Santalum ellipticum* and *S. ellipticum* var. *littorale* (Figures 3*D*, *H*, 4*H*, *I*). Stomata have been observed on both surfaces within the Santalaceae (Metcalfe and Chalk 1950). They occur only on the abaxial surface of *S. album* (Bhatnagar 1965) but on both surfaces of *S. lanceolatum* (Perrot 1927). The other Hawaiian species do not normally have stomata in the adaxial epidermis, but one silicified stoma was observed in the adaxial epidermis of *S. paniculatum* var. *pilgeri*. In *S. ellipticum*, the stomata are of the same type and

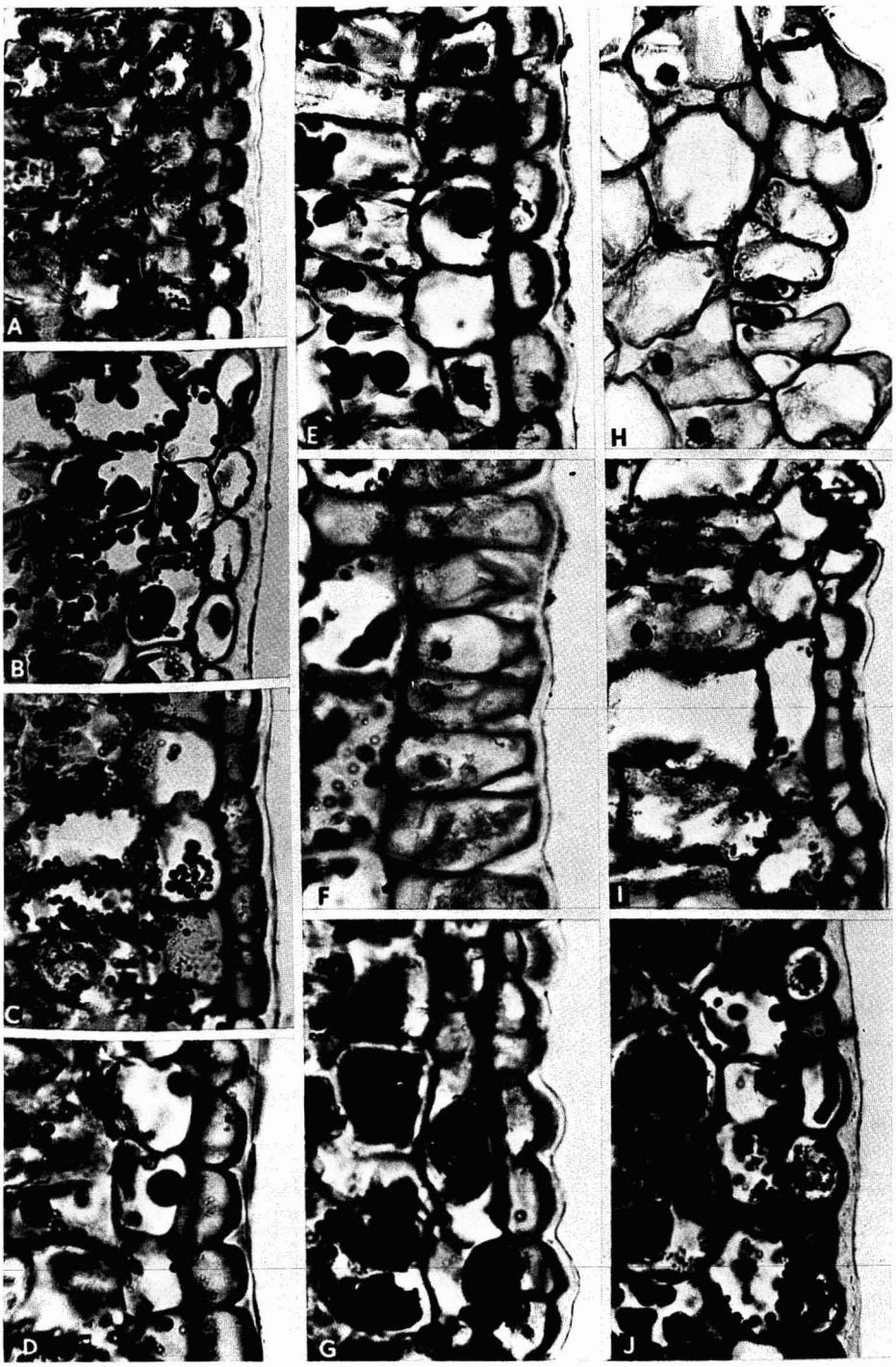

FIGURE 4. Foliar transections showing adaxial epidermis of Hawaiian *Santalum*. Notice the bottle-shaped adaxial epidermal cells in *S. haleakalae* (*F*). All ×450. *A*, *S. freycinetianum* (O'ahu) (*L. Stemmermann* 801); *B*, *S. freycinetianum* var. *pyrularium* (*L. Stemmermann* 786); *C*, *S. freycinetianum* (Moloka'i) (*L. Stemmermann* 842); D, *S. freycinetianum* var. *lanaiense* (*L. Stemmermann* 819); *E*, *S. freycinetianum* var. *auwahiense* (*L. Stemmermann* 757); *F*, *S. haleakalae* (*L. Stemmermann* 753); *G*, *S. paniculatum* (*L. Stemmermann* 703); *H*, *S. ellipticum* var. *littorale* (*L. Stemmermann* 625); *I*, *S. ellipticum* (*L. Stemmermann* 807); *J*, *S. paniculatum* var. *pilgeri* (*L. Stemmermann* 681B).

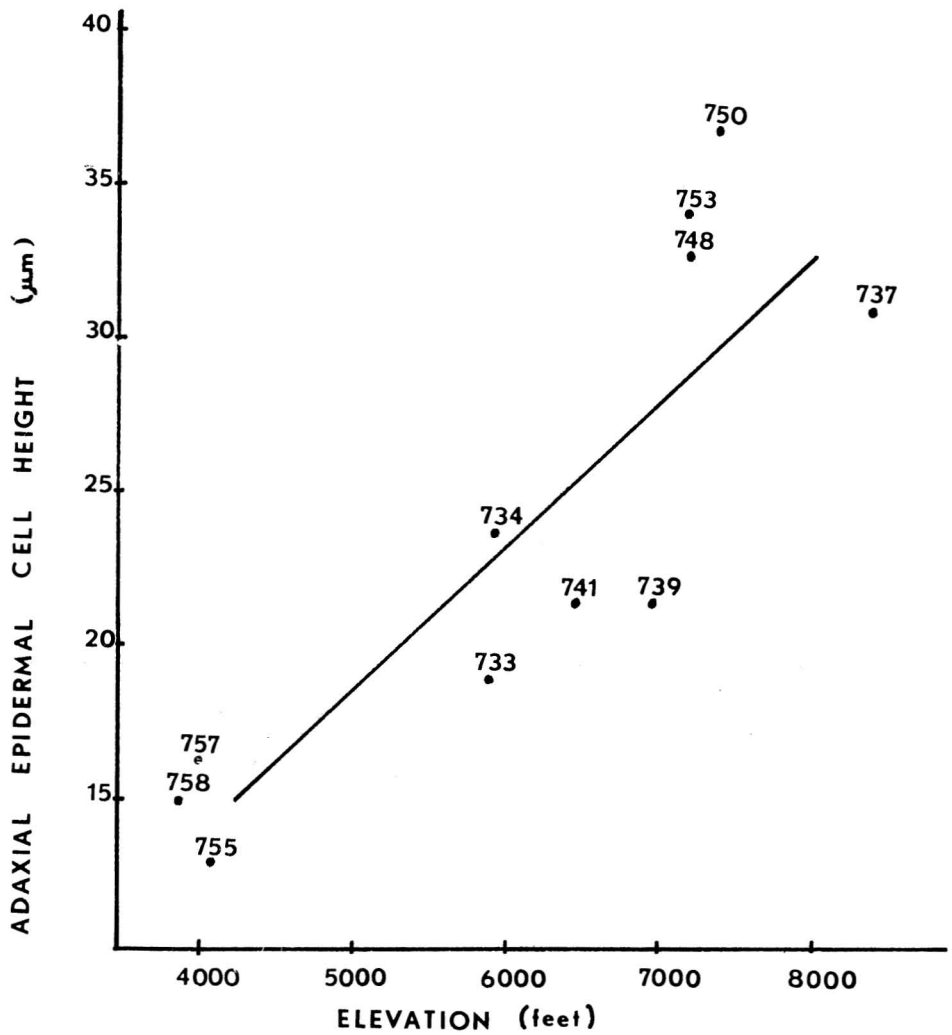

FIGURE 5. Relationship of adaxial epidermal cell height and elevation of the *freycinetianum* group of *Santalum* from Maui. Regression line: $y = 0.0046x - 4.317$; $r^2 = 0.726$; standard error of regression coefficient a_0 (y intercept), $s_0 = 5.897$; standard error of regression coefficient a_1 (slope), $s_1 = 0.0009$; significance of regression coefficient a_1, $t = a_1/s_1 = 0.0046/0.0009 = 5.11$, significant at $P = 0.001$ with df $= 9 = n - 2$.

dimensions on both leaf surfaces (Figure 6). Occasionally, these stomata are silicified and non-functional. Silicification of groups of adaxial epidermal cells occur in all taxa (Figure 7*F*) and may be a response to trauma.

MULTIPLE EPIDERMIS AND HYPODERMIS: Below the adaxial epidermis there is a single layer of hypodermis that is present in all species (Figure 8). The dimensions of the hypodermal cells are variable, but no significant differences among taxa were noted. In addition to the hypodermis in *Santalum ellipticum* var. *littorale*, occasionally there is development of a multiple epidermis and multicellular hypodermis which arises from the adaxial epidermis and normal hypodermis by periclinal divisions. Both the epidermis (especially the abaxial epidermis) and the hypodermis apparently are capable of undergoing periclinal and anticlinal divisions even in the older leaves of this taxon.

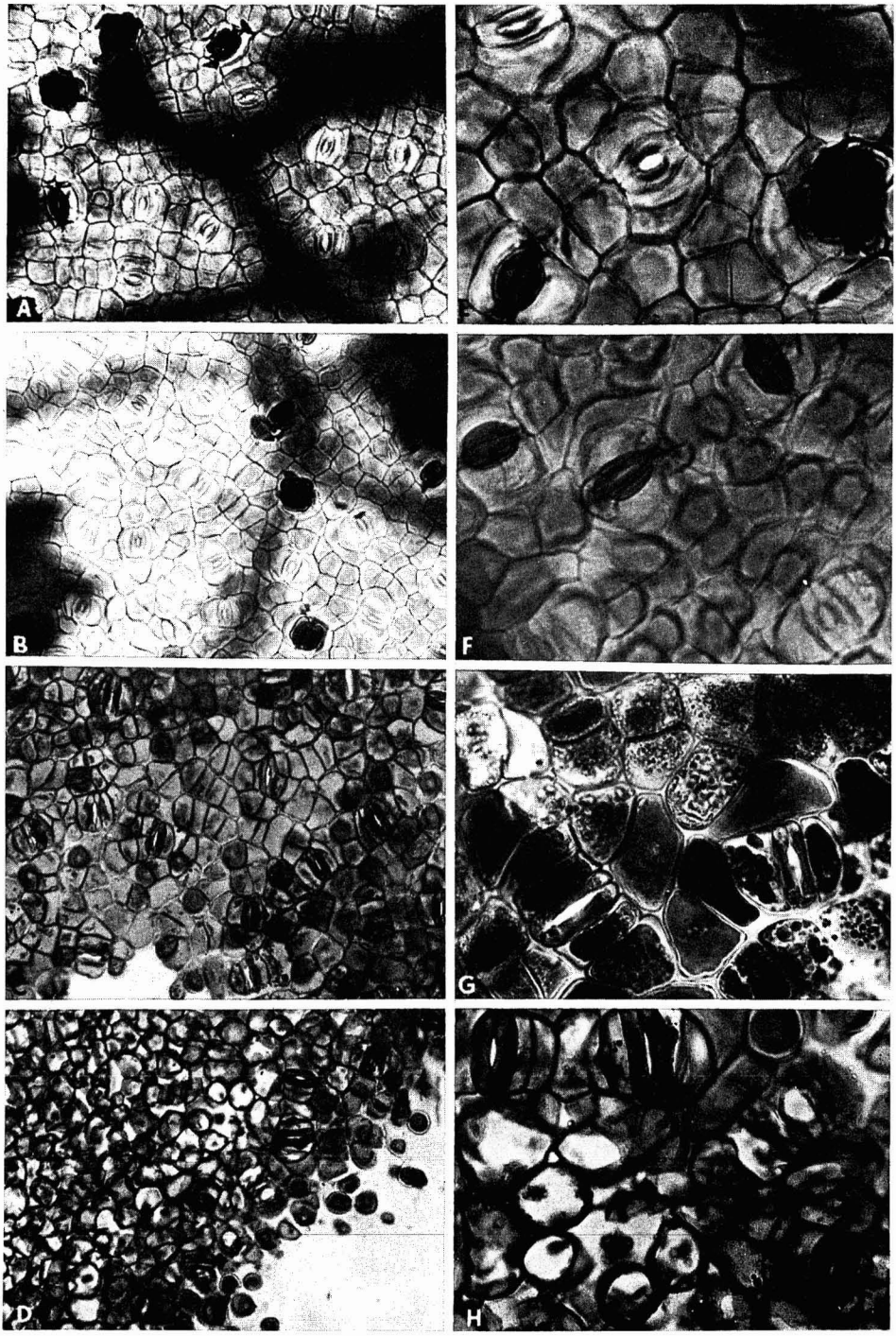

FIGURE 6. Comparison of adaxial and abaxial foliar epidermis stomata in Hawaiian *Santalum*. The similarity of adaxial and abaxial epidermis stomata in *S. ellipticum* and *S. ellipticum* var. *littorale* is illustrated. Notice paracytic subsidiary cells and random orientation of stomata in all cases. *A–D* ×177; *E–H* ×450. *A,E*, adaxial epidermis of *S. ellipticum* (*L. Stemmermann* 645); *B,F*, abaxial epidermis of *S. ellipticum* (*L. Stemmermann* 645); *C,G*, adaxial epidermis of *S. ellipticum* var. *littorale* (*L. Stemmermann* 627); *D,H*, abaxial epidermis of *S. ellipticum* var. *littorale* (*L. Stemmermann* 627).

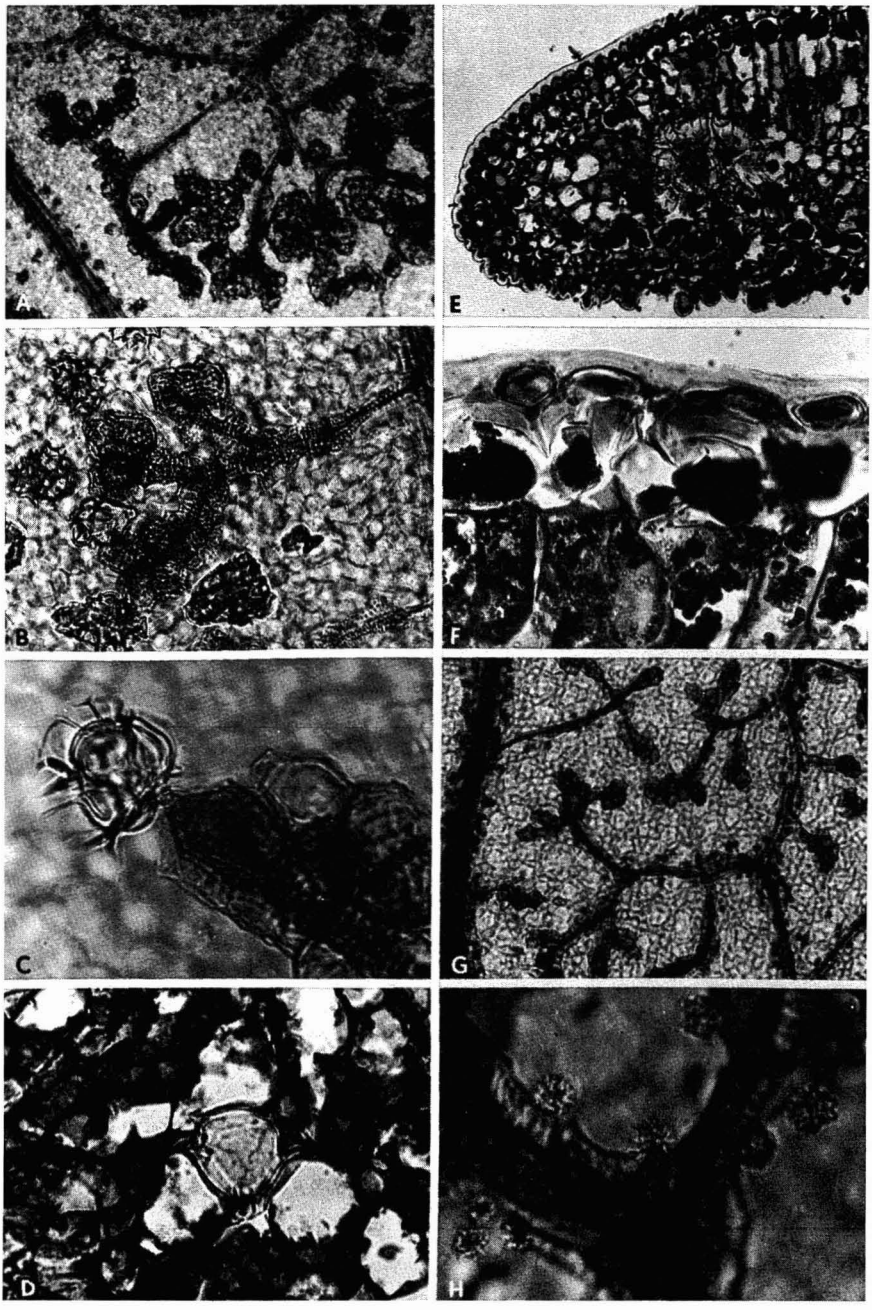

FIGURE 7. Ergastic contents in *Santalum* leaves. *A*, leaf clearing showing calcium oxalate crystals and silica bodies associated with vascular bundles in *S. paniculatum* (*L. Stemmermann* 698) ×65; *B*, leaf clearing showing silica bodies and terminal tracheids in *S. paniculatum* (*L. Stemmermann* 702) ×168; *C*, leaf clearing showing silica body and terminal tracheids in *S. freycinetianum* var. *auwahiense* (*L. Stemmermann* 754) ×425; *D*, leaf transection showing small silica body in the mesophyll of *S. haleakalae* (*L. Stemmermann* 742) ×425; *E*, leaf transection showing large silica body near leaf margin in *S. haleakalae* (*L. Stemmermann* 733) ×104; *F*, silicified upper epidermal region of *S. freycinetianum* var. *pyrularium* (*L. Stemmermann* 769) as seen in transection ×425; *G*, *S. freycinetianum* var. auwahiense (*L. Stemmermann* 754) leaf clearing showing calcium oxalate crystals associated with vascularization and lack of silica bodies in most of the mesophyll ×65; *H*, calcium oxalate crystals in *S. freycinetianum* (*L. Stemmermann* 654) as seen in leaf clearing ×425.

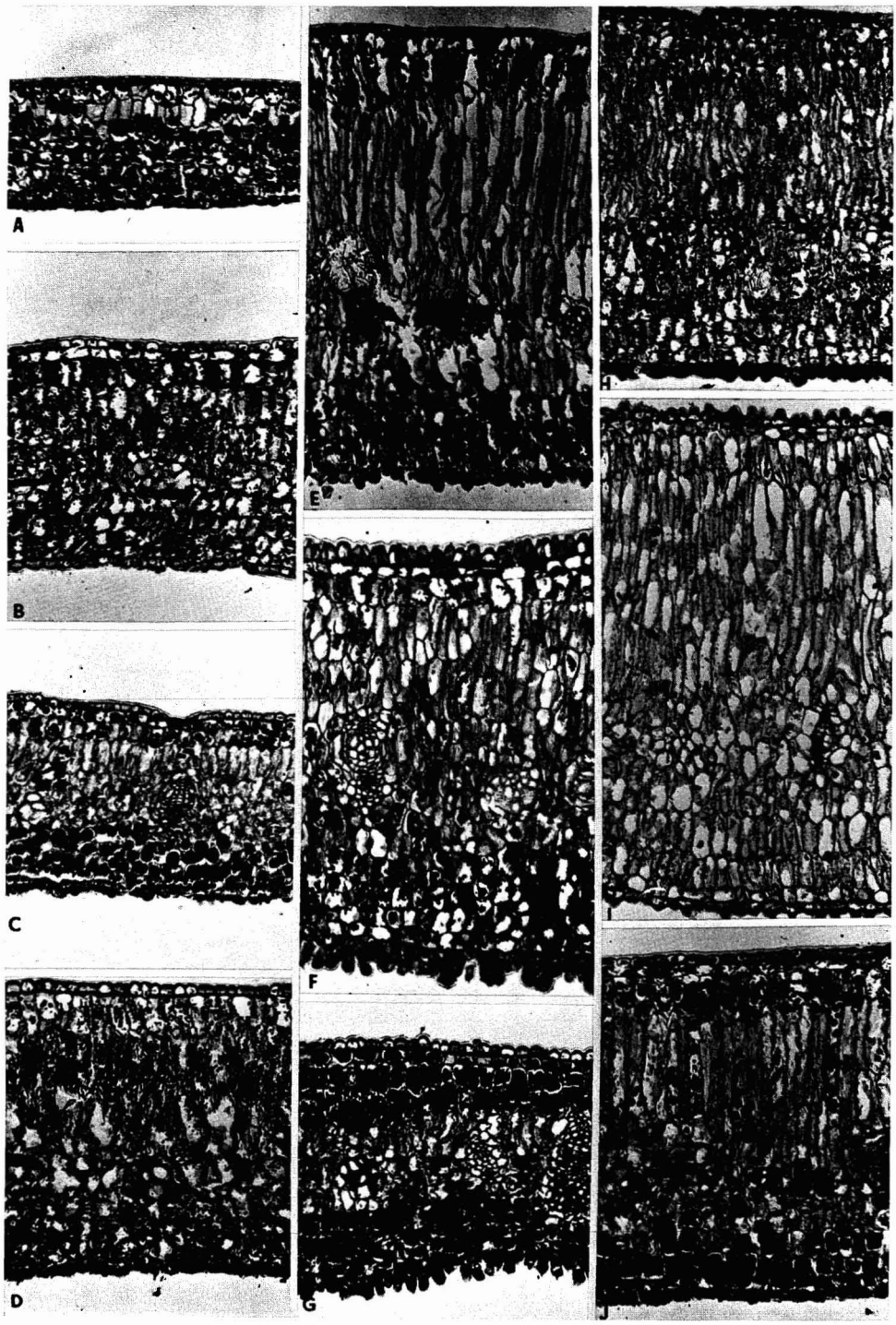

FIGURE 8. Foliar cross sections of Hawaiian *Santalum*. Notice differences in development of palisade tissue and differences in tannin distribution. All ×91. *A*, *S. freycinetianum* (O'ahu) (*L. Stemmermann* 630); *B*, *S. freycinetianum* var. *pyrularium* (*L. Stemmermann* 775); *C*, *S. freycinetianum* (Moloka'i) (*L. Stemmermann* 851); *D*, *S. freycinetianum* var. *lanaiense* (*L. Stemmermann* 812); *E*, *S. freycinetianum* var. *auwahiense* (*L. Stemmermann* 755); *F*, *S. haleakalae* (*L. Stemmermann* 750); *G*, *S. paniculatum* (*L. Stemmermann* 703); *H*, *S. ellipticum* (*L. Stemmermann* 746); *I*, *S. ellipticum* var. *littorale* (*L. Stemmermann* 627); *J*, *S. paniculatum* var. *pilgeri* (*L. Stemmermann* 681B).

MESOPHYLL: Subtending the hypodermis there is usually a layer of palisade cells intermediate in length between the cells of the hypodermis and most of the palisade parenchyma (Figure 8). Below this is the palisade layer, which can be from one to four, or rarely more, cell layers thick. Palisade cells can be quite elongate and distinct, or less distinct and transitional into the lower mesophyll, thus the leaves may be either isolateral or bifacial. Since the development of palisade tissue is greatly influenced by the environment and differences can be seen among leaves in every taxon, the thickness or number of palisade cell layers in any given leaf is of limited taxonomic value.

ABAXIAL EPIDERMIS: The abaxial epidermis exhibits distinctive characteristics in certain taxa (Figure 9). The height of the abaxial epidermal cells is a useful criterion that can be used to distinguish between the closely related *S. paniculatum* and *S. paniculatum* var. *pilgeri*. The papillate epidermal cells of *S. paniculatum* cause the abaxial epidermis to appear pale in both fresh and dried leaves. In his key to the species, Skottsberg (1927) described the lower surface of the leaves of this taxon to be powdery glaucous, but this is not the case. The abaxial epidermis of *S. paniculatum* var. *pilgeri* is not papillate, and thus does not appear pale. Similarly, the abaxial epidermal cells of *S. haleakalae* and *S. freycinetianum* var. *lanaiense* are considerably more papillate than those of the other red-flowered sandalwoods, and, as in *S. paniculatum*, these two taxa have pale abaxial leaf surfaces. Some samples of *S. freycinetianum* are also papillate and pale.

Stomata are present in the abaxial epidermis of all taxa, and their lengths are fairly uniform, as is their overall appearance. The subsidiary cells are always paracytic (rubiaceous) though occasional subsidiary cells are present that have undergone subsequent division perpendicular to the axis of the stoma. More frequently, subsidiary cells are seen which had undergone subsequent divisions parallel to the axis of the stoma as evidenced by two, or sometimes more, subsidiary cells parallel to each other. Occasionally, stomata are seen that have silicified guard cells and subsidiary cells, and are likely nonfunctional. This can occur in stomata of both leaf surfaces. The stomata in the Santalaceae have been described as being parallel to one another, and transverse to the midrib (Metcalfe and Chalk 1950), but this was not observed in any taxa. All exhibit random orientation of the stomata in respect to the leaf, however they tend to be either more or less parallel or perpendicular to adjacent stomata (Figures 3, 6).

VENATION: The venation of all taxa is camptodromous, with the secondary venation approaching the brochidodromous condition (Hickey and Wolfe 1975). Ultimately, the veins of the leaves of *Santalum* end in well-developed terminal tracheids that have scalariform to pitted thickenings and are larger than other tracheary members in the leaf (Figure 10*A*, *B*, *C*). These are present in all examined samples.

Though the development of the midrib varied considerably, a comparison made of midrib thickness and leaf thickness showed no consistent trends for any taxon, except that *S. freycinetianum* var. *lanaiense* tended to have an especially prominent midrib.

The main vascular bundle of all taxa has only abaxial phloem. Collenchyma is normally present in three areas in the midrib (Figure 10*D*, *E*): adaxial and next to the xylem and sometimes extending to the upper epidermis, abaxial and juxtaposed to the phloem, and abaxial to the phloem and adjacent to the lower epidermis. The collenchyma located next to the xylem is always present and well-developed, but in the other two positions it is well-developed in some cases and poorly so in others. Attempts to correlate development of collenchyma in these areas with taxa were not successful.

The vascularization of the petiole is similar to that of the midrib. Only abaxial phloem is present, and there is a discontinuous band of collenchyma surrounding the vascular bundle (Figure 10*F*).

ERGASTIC CONTENTS: Large isotropic masses are found in the mesophyll of most samples (Figure 7*A*, *B*, *C*, *D*, *E*), and may occasionally obscure the terminal tracheids of minor veins. These isotropic masses,

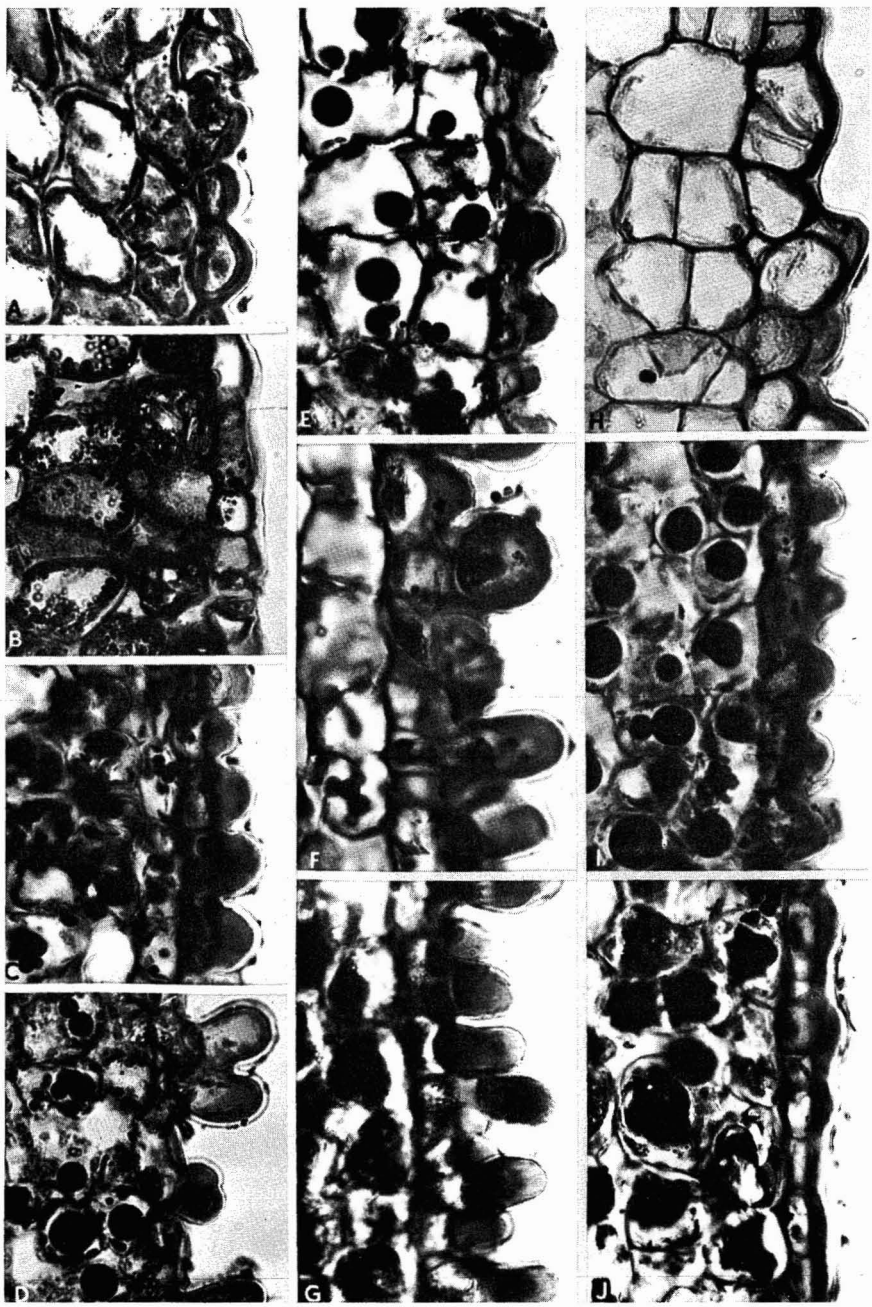

FIGURE 9. Foliar transections showing abaxial epidermis of Hawaiian *Santalum*. Notice the extreme papillate nature of the abaxial epidermis of *S. freycinetianum* var. *lanaiense* (*D*), *S. haleakalae* (*F*), and *S. paniculatum* (*G*), and development of multilayered hypodermis in *S. ellipticum* var. *littorale* (*H*). All ×425. *A*, *S. freycinetianum* (O'ahu) (*L. Stemmermann* 637); *B*, *S. freycinetianum* var. *pyrularium* (*L. Stemmermann* 786); *C*, *S. freycinetianum* (Moloka'i) (*L. Stemmermann* 842); *D*, *S. freycinetianum* var. *lanaiense* (*L. Stemmermann* 819); *E*, *S. freycinetianum* var. *auwahiense* (*L. Stemmermann* 755); *F*, *S. haleakalae* (*L. Stemmermann* 753); *G*, *S. paniculatum* (*L. Stemmermann* 703); *H*, *S. ellipticum* var. *littorale* (*L. Stemmermann* 625); *I*, *S. ellipticum* (*L. Stemmermann* 809); *J*, *S. paniculatum* var. *pilgeri* (*L. Stemmermann* 681B).

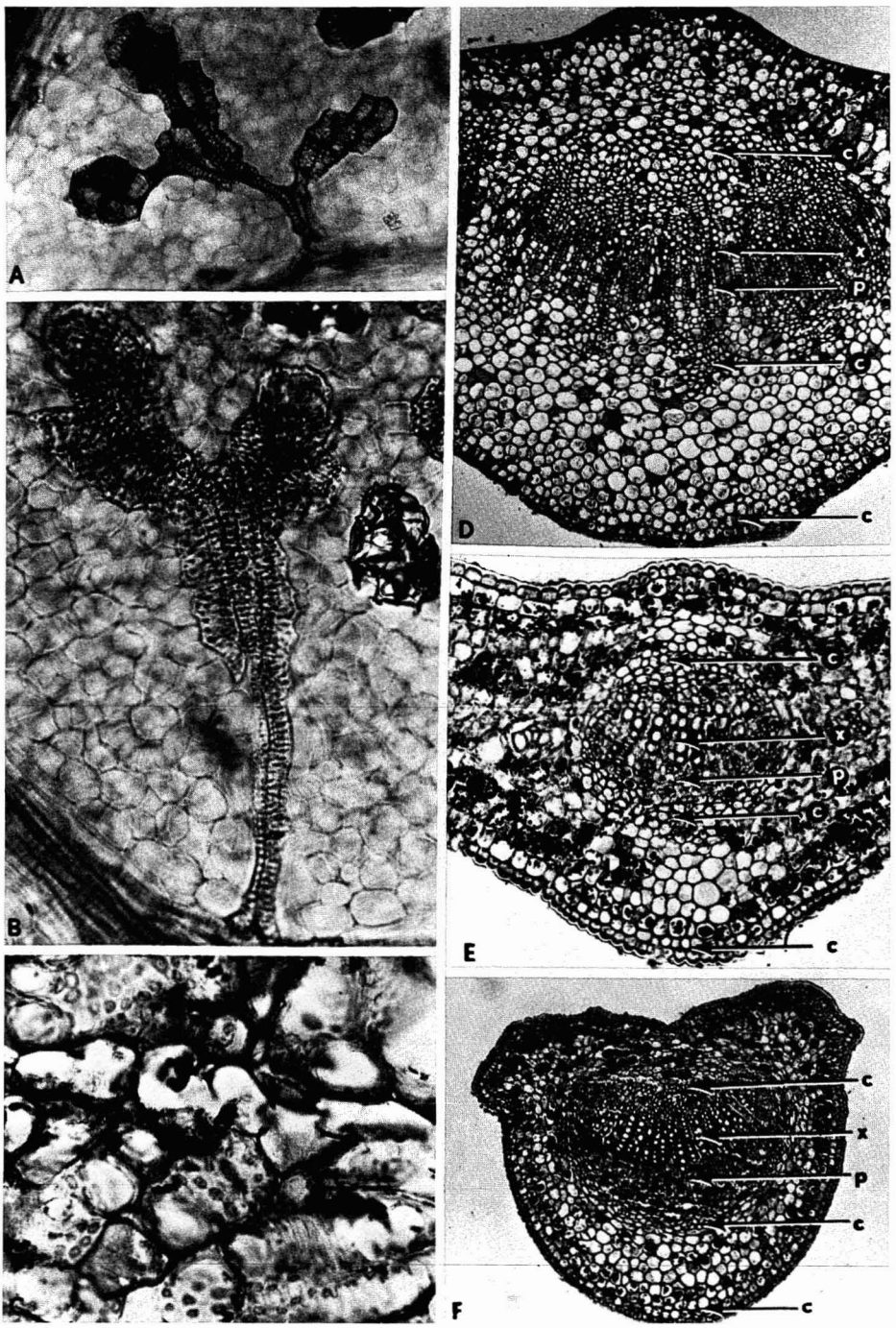

FIGURE 10. Foliar vascularization of Hawaiian *Santalum*. *A*, terminal tracheids in leaf clearing of *S. paniculatum* (*L. Stemmermann* 698) ×177; *B*, terminal tracheids in leaf clearing of *S. paniculatum* (*L. Stemmermann* 702) ×271; *C*, terminal tracheids in leaf transection of *S. haleakalae* (*L. Stemmermann* 734)—notice spiral thickenings and pits, ×450; *D*, midrib of *S. paniculatum* (*L. Stemmermann* 678)—notice abaxial phloem and abaxial and adaxial collenchyma, ×29; *E*, midrib of *S. freycinetianum* (*L. Stemmermann* 801)—notice arrangement of phloem and collenchyma similar to *D*, ×111; *F*, petiole of *S. freycinetianum* (*L. Stemmermann* 801)—notice the same arrangement of collenchyma and phloem as in *D* and *E*, ×45. ABBREVIATIONS: x = xylem, p = phloem, c = collenchyma.

TABLE 1

SILICA ANALYSIS OF SOME SAMPLES OF *Santalum* LEAVES

COLLECTION NUMBER	SPECIES	ASH WEIGHT (% dry wt)	RESIDUE AFTER NITRIC ACID TREATMENT (% dry wt)	RESIDUE AFTER NITRIC ACID TREATMENT (% ash wt)
745	*S. ellipticum*	13	4	31
746	*S. ellipticum*	13	6	50
761A	*S. ellipticum*	17	10	57
738	*S. haleakalae*	14	7	52
801	*S. freycinetianum*	10	4	40
812	*S. freycinetianum* var. *lanaiense*	12	8	63

which may exceed 225 μm in diameter, appear to be groups of cells with walls that have become silicified. Such structures have previously been reported in Santalacean genera (Solereder 1908, Haberlandt 1914, Metcalfe and Chalk 1950). The groups of cells are often associated with the terminal tracheids (Figure 7*A*, *B*, *C*). The presence of these masses is not a useful taxonomic characteristic as it may be affected by the age of the leaf or environmental conditions, including soil fertility, and such conditions could not be controlled in sampling. These silicified masses do not dissociate easily, even following treatment with a hydrogen peroxide–glacial acetic acid macerating solution. Thus, it was difficult to determine the shape of the individual cells, although they appear to be spherical, with sharp protuberances that hold the mass of cells together. These bodies, while often distributed throughout the lamina of the leaf, were not observed in all samples, but are usually present toward the margins of a leaf even if absent elsewhere in the lamina.

Other patterns of silicification are also evident. In many instances silicified guard cells are present (Figure 6*A*, *B*, *E*, *F*), and occasionally entire areas of either epidermis may be silicified (Figure 7*F*). When this occurs, silicification either may be restricted to the epidermis or may extend into the mesophyll.

The percent silica per dry weight and ash weight was calculated for a few samples chosen for analysis because they appeared to have especially large numbers of silica bodies. Analysis showed that the silica in some of these extreme cases could account for up to 10 percent of the dry weight of the leaf and for more than 50 percent of the ash weight of the leaf (Table 1). The percent silica noted is high in terms of normal silica content of leaves for most plants, but higher values have been observed in analysis of silica content of the leaves of certain grasses (Lanning, Ponnaiya, and Crumpton 1958).

Other ergastic materials readily apparent in leaf clearings are druses, which may be associated with the vascular system (Figure 7*G*, *H*). These crystals were not observed in every sample, but their presence, absence, abundance, or distribution within a leaf were not useful taxonomic criteria since their distribution is not always consistent even within a single population.

Dark-staining masses, presumably tannins, are distributed throughout both the young and mature leaves of most taxa, though they are lacking in *S. ellipticum* var. *littorale*. Sometimes the tannins are restricted to specific tissue layers within a leaf (Figure 8), but any patterns of differential distribution of tannins are not consistent within a leaf, far less within a taxon. Tannins can be found in virtually all tissues in the leaf though they are often lacking in the upper epidermal cells, and may not be abundant in the palisade cells.

DISCUSSION

Wood

Description and reports of the variability of the cellular components of wood have been made for the Hawaiian taxa of the

TABLE 2

VULNERABILITY AND MESOMORPHY INDICES OF THE TAXA *Santalum*

SPECIES	VULNERABILITY INDEX = VESSEL DIAMETER ÷ VESSELS/mm^2	MESOMORPHY INDEX = VULNERABILITY INDEX × VESSEL LENGTH
S. freycinetianum var. *pyrularium*	1.2	436.8
S. freycinetianum (Oahu)	1.8	611.0
S. freycinetianum (Molokai)	0.8	233.3
S. freycinetianum var. *lanaiense*	0.8	227.9
S. haleakalae	0.6	194.2
S. ellipticum	0.8	243.5
S. paniculatum	0.7	235.8
S. paniculatum var. *pilgeri*	1.1	436.3

genus *Santalum*. The data collected were generally in agreement with previous, but incomplete, work done within the genus and family (Brown 1922, Metcalfe 1935, Swamy 1949, Metcalfe and Chalk 1950).

The most notable features of the wood that were found in this study are the structures on the walls of vessels that resemble lateral perforations. This study has not adequately characterized these structures, and they apparently have been overlooked by previous authors. Future study is necessary to determine the nature of these structures and to determine their relationship to other components of the wood.

No features of wood morphology were found that could clearly separate any of the taxa. The variation within samples of a species, attributable to differences in the age and position of the sample on the plant, as well as environmental differences in the habitats of the plants sampled, are sufficient to obscure the differences among taxa. These problems of variability within samples have been addressed in the past (Rendle and Clarke 1934, Stern and Greene 1958, Fritts 1966, Sastrapradja and Lamoureux 1969).

Brown (1922) mentions that *Santalum paniculatum* var. *pilgeri* (referred to by him as *S. freycinetianum*) can be distinguished from *S. freycinetianum* var. *pyrularium* by having less abundant resinlike material and the "imperfect occurrence in *S. freycinetianum* var. *pyrularium* of short crystal containing parenchyma, and thick walled wood parenchyma." His conclusions are likely an artifact of small sample size (three of each), as these features have not been found to be reliable means of distinguishing the taxa.

Carlquist's (1977*a*, 1977*b*) formulas were used to calculate the vulnerability index (vessel diameter ÷ vessels/mm^2) and the mesomorphy index (vulnerability index × vessel length). The average total vessel member length, tangential diameters of vessels, and vessels/mm^2 for each taxon were used in these calculations (Table 2). Carlquist (1977*b*) suggests that vulnerability values less than 1.0 reflect a greater chance of survival under water stress than values greater than 1.0. Furthermore, he suggests (1977*a*) that the lower the mesomorphy index, the greater the degree of xeromorphism exhibited. The indices obtained for the species of the genus *Santalum* imply that *S. haleakalae* from arid subalpine Haleakalā expresses more of a xeromorphic nature than do the other species, and that *S. freycinetianum* from O'ahu is the most mesomorphic of the group. No precise climatological data are available for the collection sites (Taliaferro 1959) to determine the validity of these conclusions, but they do not seem unreasonable based on general observations of the collection sites, as well as the xerophytic nature of the leaves (Hanson 1917, Fahn 1964) of *S. haleakalae*, which are small and thick in comparison to the thin large leaves of the mesomorphic *S. freycinetianum*. It is interesting that those taxa with the lowest vulnerability and mesomorphy indices based on wood morphology have other xeromorphic features. In Figure 9, it can be seen that *S. freycinetianum* from

Moloka'i, *S. freycinetianum* var. *lanaiense*, *S. haleakalae*, *S. ellipticum*, and *S. paniculatum*, all with vulnerability indices less than 1.0 (Table 2), have papillate lower epidermal cells that may function in reducing transpiration. Unfortunately, it is not possible to determine how large a difference in the index values is significant until further work is done using the indices within genera and populations.

Leaves

Foliar morphology has been described for representative samples of the recognized taxa examined. Only *Santalum ellipticum* and *S. ellipticum* var. *littorale* have stomata in the adaxial as well as abaxial epidermis; the other members of the *ellipticum* group and all members of the *freycinetianum* group have only abaxial stomata. This finding supports the retention of *S. paniculatum* and *S. paniculatum* var. *pilgeri* as distinct from *S. ellipticum*, contrary to the opinions of Degener (1937) and Fosberg (1962), who have recognized these two taxa as varieties of *S. ellipticum*. The presence of stomata in the epidermis of only *S. ellipticum* may in fact imply an origin of *S. paniculatum* and *S. paniculatum* var. *pilgeri* independent from *S. ellipticum*.

Stomata have been reported in both epidermal surfaces of *Santalum lanceolatum* (Perrot 1927) and restricted to only the abaxial epidermis in *S. album* (Bhatnagar 1965). No information is available concerning stomatal distribution of the other species of the genus. With this in mind there are several possible explanations of the evolution within the green-flowered taxa. There may have been one introduction with stomata on both surfaces that gave rise to the species with stomata on a single surface, or there may have been separate introductions of both types. There may also have been an introduction of plants with stomata on one surface that evolved to *S. ellipticum* with stomata on both surfaces. But this seems unreasonable since *S. ellipticum* occurs throughout the archipelago while *S. paniculatum* and *S. paniculatum* var. *pilgeri* are restricted to the island of Hawai'i, and presumably the ancestral form would not be restricted to the youngest island.

The degree to which the presence of stomata on the adaxial surface should be considered to be under genetic as opposed to ecologic influence is not known. Experiments have shown that inhibition of stomatal development is possible (Cutter 1969). Without having done a detailed analysis of the morphological similarities between the extra-Hawaiian and Hawaiian species of *Santalum*, it is not possible to ascertain which of the possible pathways were effective in the evolution of *S. paniculatum* and *S. paniculatum* var. *pilgeri*. However, since successful dispersal to the Hawaiian Islands is an improbable event, and the inhibition of stomatal development has been experimentally altered, it is likely that there was one introduction of the green-flowered sandalwoods, the ancestral form having stomata on both surfaces, followed by evolution to taxa that have stomata only on their abaxial epidermis. The findings of a single stoma on the adaxial epidermis of one of the examined samples of *S. paniculatum* var. *pilgeri* further indicates that the genetic capability or the differentiation of stomata on the adaxial surface of the leaves of that taxon is present, but not usually expressed.

There are morphological criteria for separating *Santalum paniculatum* and *S. paniculatum* var. *pilgeri*. The cells of the abaxial epidermis of *S. paniculatum* are papillate, and thus the abaxial surface appears pale. This is readily seen in both herbarium and fresh specimens, and is not caused by a powdery glaucousness as has been described by previous authors. The abaxial epidermis of *S. paniculatum* var. *pilgeri* is not papillate, and therefore is not pale.

Within the *freycinetianum* group, significant findings in terms of foliar morphology include the bottle-shaped adaxial epidermal cells of *Santalum haleakalae*. While it has been demonstrated that the height of these cells is somehow related to high altitude, the factors responsible for such cell formation have not been identified.

The abaxial epidermal differences were

noted as taxonomically useful criteria in both the *ellipticum* and *freycinetianum* groups of the genus. Within the *freycinetianum* group, *Santalum haleakalae* and *S. freycinetianum* var. *lanaiense* have papillate abaxial epidermal cells, and therefore the abaxial surfaces of the leaves of those taxa appear pale. Occasionally, the other red-flowered taxa also have pale abaxial surfaces and papillate epidermal cells. Based solely on foliar morphology, *S. freycinetianum* var. *lanaiense* and *S. haleakalae* are the only taxa of the *freycinetianum* group that can be distinguished from the other taxa of that group. Furthermore, no consistent differences could be found that could separate the *ellipticum* and *freycinetianum* groups from each other based on foliar morphology alone.

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