ANATOMICAL STUDY OF LEAF AND STEM OF FORMOSAN *PITTOSPORUM*, AS AN ECOLOGICAL IMPLICATION[1]

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Abstract:

Pittosporaceae is exculsively native to the Old World. There is only one genus, *Pittosporum*, with five species and a variety in Taiwan. They are found from lowland (*P. tobira*, *P. pentandrum* and *P. moluccanum*), through median (*P. illicioides* in part) to high altitudes (*P. illicioides* in part, *P. illicioides* var. *angustifolium* and *P. daphniphylloides*). Except for the cultivated *P. pentandrum which* will grow into a small tree, most species of Formosan *Pittosporum*, including the wild *P. pentandrum* are small or large shrubs. They are all mesomorphic but more or less tend to be xeromorphic.

Carlquist (1977) introduced vulnerability and mesomorphy ratios to indicate the reflection of vessel elements under various ecological conditions. In Pittosporaceae as a whole, both the vulnerability ratios and mesomorphy ratio of Formosan *Pittosporum* are low. All alpine species, have low values of the ratio of palisade tissue to intercellular space; only *P. daphniphylloides* has a thick cuticle. Thus, the low figures of both ratios may reflect adaptation to a form of physiological drought, caused by the winter frost. For the lowland species, the thicker cuticle, the low figures for both ratios, may be by an adaptation to the high temperatures, sunny weather and long period of drought in summer.

The study of anatomical characters of leaves and stems for Taiwan *Pittosporum* indicate that plants of the same species vary in anatomical characters when they grow in different environmemtal conditions, while different species, growing close together or under similar environments, have similar anatomical characters.

INTRODUCTION

There are nine genera and about two hundred and fourty species listed in Pittosporaceae in the Old World. The number of valid species in *Pittosporum* is expected to be about 200 (Carlquist, 1981). There is only one genus, *Pittosporum*, in Taiwan. According to Li (1977), five species, namely *P. daphniphylloides* Hayata, *P. tobira* Ait., *P. illicioides* Makino, *P. pentandrum* (Blanco) Merr. and *P. moluccanum* Miq. have been recorded. Later on, a variety, *P. illicioides* var. *angustifolium* Huang ex Lu was added (Lu, 1977).

The general growth form of Formosan *Pittosporum*, is the same as Hawaiian and

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New Caledonian species described by Carlquist (1981). These often have numerous, long, sparsely branched stems. Except for the cultivated *P. pentandrum* which will grow into a small tree, most species of Formosan *Pittosporum*, including the wild *P. pentandrum*, are small or large shrubs. In addition, *P. daphniphylloides* shows a pseudoepiphytic habit. Carlquist (1981) has made a study of wood anatomy of Pittosporaceae, including 62 collections from 48 species. He found that plants of the Pittosporaceae grows in regions of great aridity and also in wet montane areas. Thus he suggested that the family should be an ideal group for analyzing the relationship between ecology and wood anatomy. The range in habit and habitat of Formosan *Pittosporum* is also wide. *P. daphniphylloides* occurs in broad-leaved forests at altitudes of 1700-2000 m high, in the central and western parts; *P. illicioides* and its variety, are common in broad-leaved forests at medium to high altitudes; *P. moluccanum* is known only from S. Cape and the Island Lanyu, in thickets along the seashores; *P. pentandrum* is found along the seashores and the coastal regions in the Hengchun Peninsula; *P. tobira* is very common along the coastal regions of northern Taiwan.

As a general rule, the structures of both stems and leaves are usually influenced by the environment (Esau, 1965, 1977; Jackson, 1967; Turrell, 1939, 1944; Wylie, 1939, 1943, 1946). In the past, there was only a brief discussion of wood anatomical characters of *P. tobira* by the second author (Huang, 1965. *f.2 G-1*) in Taiwan. This paper deals with the anatomical characters of both stems and leaves of all Formosan *Pittosporum* taxa. A further consideration of the ecological implications are discussed. Many anatomical characters are quantified and discussed.

MATERIALS AND METHODS

Twelve wood collections from five species and one variety were studied (Table 1). Dried wood samples were subdivided and boiled preparatory for sectioning and maceration. Wood sections were prepared by the celloidin method (modified from J. E. Sass 1951) and stained with safranin and Hematoxylin (Merck Co.). Macerations were prepared with superoxal fluid and stained with safranin. Mean values are based on 50 measurements each, except for vessels per sq. mm and libriform fiber diameter, which are based on ten measurements each.

Twelve leaf collections from five species and one variety were studied by methods of transections and the clearing technique (Table 2). Ten random selection of mature leaves per each collection were prepared for each study. Pieces of 1 by 1-cm were cut crosswise through the middle, the widest and the portion near petiole of each leaf were fixed in FAA solution and processed through customary procedures of dehydration, infiltration and embedding. Sections cut at a thickness of 8-10 μm were stained with Hematoxylin and safranin. For the clearing technique, the 1 by 1-cm pieces were processed through the standard clearing procedures (Tsai, 1975 in Chinese). The area percentage of spongy tissue, palisade tissue and intercellular space were measured by method modified from Parkhurst (1982). Means are based on 25 readings. For measurement of stomatal index (SI), a minimum area of 0.5mm^2 was made (Hill, 1980).

Table 1. Wood features of Formosan *Pittosporum*

Species	Collection No.	Habitat altitudes (m)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Pittosporum daphniphylloides Hayata	T.C.Huang 9958	Mixed forest,2160m	1.62	34	175	385	550	1.43	2.7	.19	74	204	106	+	0	mv,wv	0
	T.C.Huang 10000	raodside, 1600m	2.84	28	368	414	615	1.49	2.2	.08	32	198	91	+	0	mv,wv	0
P. illicioides Mak.	T.C.Huang 9809	dense forest, 2150m	2.20	30	269	409	596	1.46	2.7	.11	45	230	137	+	0	mv,wv	0
	T.C.Huang 9877A	roadside, 620m	2.20	34	329	395	642	1.63	3.6	.10	41	223	106	+	.w.	mv,wv	0
P. illicioides Mak. var *angustifolium* Huang ex Lu	T.C.Huang 9807	dense forest, 2150m	2.54	28	254	437	676	1.55	3.5	.11	48	183	102	+	.w.	mv,wv	0
P. moluccanum Miq.	Hsieh s.n.	under *Timonius arboreus* 100m	1.88	36	192	386	680	1.76	2.4	.19	72	202	105	+	b.w.s	0	+
P. pentandrum (Blanco) Merr.	*FPAW-610		2.04	74	64	776	1034	1.33	4.1	1.16	899	432	97	+	w.s	0	??
	L.S.Chern 73	semi-open area, 50m	1.80	41	145	354	585	1.65	3.0	.28	99	196	124	0	b.w.s	0	0
	L.S.Chern 66	cult. NTU,50m	2,40	66	143	415	658	1.59	2.5	.46	192	192	97	0	b.w.s	0	0
P. tobira (Thunb.) Ait.		*cult. Claremont	3,16	31	204	500	625	1.25	1.8	.15	75	239	85	+	B.w.	mv,wv	??
	L.S.Chern 62	coastal area, 50m	2.45	33	203	375	649	1.73	2.5	.16	61	219	102	+	o	wv	0
	L.S.Chern 64	coastal area, 50m	2.04	37	234	383	662	1.73	2.7	.16	61	169	85	+	b.w.	wv	0

* : Data read from Carlquist (1981).

Key to columns: 1, Number of vessels per group as seen in transection, mean. 2, Vessel diameter, mean, μm. 3, Number of vessels per sq. mm. of transection, mean. 4, Vessel element length, mean, μm. 5, Imperforate element length, mean, μm.6, Ratio, mean imperforate element length divided by mean vessel element length. 7, Imperforate element wall thickness, mean, μm. 8, "Vulnerability" ratio (vessel diameter divided by vesssel per sq. mm.). 9, "Mesomorphy" ratio (vulnerability ratio multiplied by vessel element length). 10, Multiseriate ray height, mean, μm. 11, Uniseriate ray height, mean, μm. 12, Helical sculpture on walls of secondary xylem vessels; +=present, 0=absent. 13, Occurrence of rhomboidal crystals in rays; W=crystals present in wings; B=crystals present in body of ray; S=subdivided wing cells containing crystals present. Upper case letters= crystals abundant; lower case letters=crystals infrequent. 0=no rhomboidal crystals observed. 14, Growth ring phenomena: mv=vessels more numerous in early wood than in late wood; wv=vessels wider in early wood than in late wood; 0=no appreciable growth ring activity present. 15; Starch grains in wood ray cells or libriform fibers: +=present, 0=absent,?? unknown.

Table 2. Some leaf features of Formosan ***Pittosporum***:

Species	Collection	Habitat	1A	1B	1C	2A	2B	2C	3A	3B	3C	4A	4B	5A	5B	6	7
Pittosporum daphniphylloides Hayata	T.C.Huang 9957	dense forest, 2160m	28	26	46	24	32	44	191	683	22	3.2	2.6	3.1	77	308	++
	T.C.Huang 9958	as above	28	28	45	27	34	39				3.2	2.6	3.4	72	269	++
	T.C.Huang 10000	roadside, 1600m							204	690	23						
P. illicioides Mak.	T.C.Huang 9810	dense forest, 2150m	42	26	32	40	31	30	139	756	16	1.2	0.8	4.4	45	165	0
	T.C.Huang 9877A	roadside, 620m	49	30	22	50	32	19	158	725	18	2.0	1.3	4.8	56	156	0
P. illicioides Mak. var.	T.C.Huang 9807	dense forest, 2150m	32	23	45	29	27	44	111	468	19	0.8	0.5	4.2	36	174	0
angustifolium Huang ex Lu	T.C.Huang 9808	as above	40	24	36	40	25	35	122	554	18	1.3	0.7	4.4	43	190	0
P. moluccanum Miq.	Hsieh s.n.	under *Timonius arboreus* 100m	28	46	26	26	49	25	229	667	26	2.6	2.2	3.6	31	218	0
P. pentandrum (Blanco) Merr.	L.S.Chern 71	semi-open area, 50m	53	40	7	51	38	6	260	822	24	2.0	2.1	4.9	65	239	++
	L.S.Chern 66	cult. NTU, sunny 50m	56	35	9	61	30	9	218	882	20	2.8	2.5	4.5	81	180	++
P. tobira Ait.	L.S.Chern 62	coastal area (sunny), 50m	30	40	31	31	43	30	159	690	18	3.3	2.4	4.3	67	244	+
	L.S.Chern 64	coastal area (semi-open) 50m	28	43	29	25	46	29	176	618	22	3.0	2.4	4.1	67	242	+

Key to the columns: 1, Percentage of the component area near the maximum width of the leaf. 1A=palisade tissue; 1B=spongy tissue; 1C=intercellular space. 2, Percentage of the component area near the petiole. 2A=palisade tissue; 2B=spongy tissue, 2C=intercellular space. 3, Stomatal index. 3A=number of stomata in a given area (about $0.5mm^2$) 3B=number of epidermal cells in the same area in 3A; 3C=stomatal index=3A/3B multiply 100. 4, Thickness of cuticle layer, mean, μm. 4A=adaxial epidermis; 4B=abaxial epidermis. 5, Vein density. 5A=number of veins seen in transection (c.a. 1.3mm in width of view); 5B=percentage of bundle sheath in 5A. 6, Thickness of leaf, mean, μm. 7, 2-layered epidermis, ++=occur frequently; +=occur infrequently; 0=not observed.

RESULT

1. Wood characters:

As shown in nearly all of the transections, vessels in Formosan *Pittosporum* tend to be rounded rather than angular in outline (figs. 4, 7, 13, 16, 18, 19, 22, 23, 26, 29). Vessels range from mostly solitary to aggregated in small groups. The figures in Table 1 (column 1) reflect this clearly. Among all species studied, both the highest and lowest figures occurred in *P. daphniphylloides*. The highest figure (2.84) was found in the roadside collection while the lowest (1.62) belongs to the mixed forest collection. Most species, such as *P. tobira* (fig. 4), *P. pentandrum* (fig. 7), *P. moluccanum* (fig. 13), show a random arrangement in vessel grouping. In. *P. pentandrum*, in addition to this random type, vessel groupings of more or less radial arrangement are also found (fig. 8). Diagonal and tangential patches are very common in *P. daphniphylloides* (fig. 18, 19). When *P. illicioides* grows under dense forest, the vessels not only concentrate in the early wood, but also show a radial patch arrangement (fig. 23). The vessels of *P. illicioides* var. *angustifolium* growing nearby are in diagonal and radial patch configurations (fig. 26). Vessel groupings in the *P. illicioides*, growing along roadsides at medium altitude, are mostly in a diagonal and tangential patch pattern (fig. 29). It seems that the growth rings are less obvious in collections with vessel groupings of more random arrangement (figs. 4, 7, 8, 13).

The average vessel diameter for Pittosporaceae studied by Carlquist (1981) was 42.2 μm. In all Formosan *Pittosporum*, except *P. pentandrum*, the vessel diameters are less than 40 μm. Wide vessels occur in *P. pentandrum*, including collections in both present and Carlquist's (1981) studies. Vessel diameter, vessel element length and vessel density (number of vessels per sq. mm of transection) have been combined into ratios termed the vulnerability ratio (vessel diameter divided by vessels per sq. mm) and mesomorphy ratio (the vulnerability ratio multiplied by vessel element length). Figures for these ratios are given for Formosan *Pittosporum* in Table 1. These ratios, created recently by Carlquist (1977), are proving to be useful indicators within certain limits (Carlquist, 1980a, 1981, 1982). In *P. tobira*, the two collections from the same locality have the same values in both ratios. *P. illicioides* and *P. illicioides* var. *angustifolium*, under the same dense forest, have the same vulnerability ratio (0.11) and very close figures for the mesomorphy ratio (45 for *P. illicioides*, 48 for the other). In *P. pentandrum*, figures for both ratios for collection from National Taiwan University Campus (open area) are larger than those for semi-open area of Ping-Tung collection. In *P. daphniphylloides*, figures for both ratios for dense-forest collection (Alishan) are larger, more or less, than those for roadside collections (Chiti).

Perforation plates of Pittosporaceae have been reported to be exclusively simple (Metcalfe and Chalk, 1950), and with only one exception, *Pittosporum paniense*, in Carlquist's study (1981). All perforation plates in Formosan *Pittosporum* are indeed simple (figs. 9, 21, 22) and the lateral wall pitting of vessels for all species studied have an alternate pattern (figs. 6, 9, 17, 20, 28, 30). Helical sculpturing (tertiary helical thickenings) occurs on vessels of all Formosan *Pittosporum* studied (figs. 5, 6, 20, 21, 22, 25, 28), except for *P. pentandrum* (figs. 9, 12). In both different collections of Formosan *P. pentandrum*, no helical sculpture on vessels was found. While in the collection from Philippines, the helical sculpture on vessels has been observed (Carlquist, 1981; table 1).

Both the presence of vestigial borders and the absence of them on the imperforate tracheary elements are reported for Pittosporaceae by Metcalfe and Chalk (1950). In present study, as no bordered pits observed, the imperforate tracheary elements may be designated as libriform fiber (fig. 17). All libriform fibers observed in this study are almost septate (figs. 5, 6, 11, 12, 17, 20, 21, 24, 27, 28, 30).

The basic axial parenchyma type in Formosan ***Pittosporum***, as noted by Metcalfe and Chalk (1950) and Carlquist (1981) in Pittosporaceae as a whole, is scanty paratracheal. A few cells are adjacent to vessels or vessel groups, as seen in transections. Strands of axial parenchyma mostly range from four to seven cells (figs. 6, 20), as seen in Carlquist's study (1981). Rays in Pittosporaceae as seen in tangential sections have been described as narrow, two to three cells wide when multiseriate (Carlquist, 1981). Among the species of Formosan ***Pittosporum***, only the roadside ***P. illicioides*** has wider multiseriate rays, sometime more than 3 cells in width (fig. 30). Most rays of other collections are narrow, uniseriate, or multiseriate with only two to three cells in width (figs. 5, 6, 12, 17, 20, 25, 28). Besides, in ***P. illicioides*** and ***P. illicioides*** var. ***angustifolium*** under the same dense forest, both seem to have more uniseriate rays than other collections studied (figs. 25, 28). Ray histology in Formosan ***Pittosporum*** is rather uniform and can be expressed simply, as seen in other taxa of Pittosporaceae (Carlquist, 1981).

Uniseriate rays are composed of upright and square cells (figs. 11, 27); the wing cells of the multiseriate rays are equivalent to uniseriate rays, composed of upright and square cells (figs. 10, 11, 15, 21, 24, 27). The body cells in multiseriate rays are procumbent (figs. 10, 11, 15, 21, 24, 27). In collections with much uniseriate rays, i. e. under dense forest ***P. illicioides*** and ***P. illicioides*** var. ***angustifolium***, the procumbent cells tend to be more square (figs, 24, 27). In other words, the wider the ray, the more numerous the procumbent cells and the more radially elongated they are. Erect cells in wings of multiseriate rays of ***P. moluccanum*** and ***P. pentandrum*** may occasionally be subdivided horizontally (figs. 10, 11, 15), but otherwise they are like ordinary erect ray cells. Such subdivided erect ray cells were observed in many other taxa of Pittosporaceae (Carlquist, 1981). Ray cell are lignified in Pittosporaceae (Metcalfe & Chalk, 1950).

Druses have been reported from various vegetative cells of Pittosporaceae (Metcalfe and Chalk, 1950; Hass, 1977). As seen in present study, abundant druses, but rarely styloid and raphides, may be found in the leafy tissue (fig. 32). Although druses may be seen in pith cells (fig. 14), no druses can be observed in the secondary xylem. In the secondary xylem, rhomboidal crystals were sometimes observed within the vessel elements or libriform fibers, and they most often occur in the ray parenchyma. Crystals in rays may sometimes occur in body cells or subdivided wing cells of multiseriate rays (figs. 10, 11, 15), but most often occur in erect wing cells or uniseriate ray cells (figs. 10, 11, 27).

The ***P. tobira***, cultivated in Claremont, introduced from Japan, has abundant rhomboidal crystals in both body cells and wing cells of multiseriate rays (Carlquist, 1981). But there is scanty or even none of crystals observed in secondary xylem of both collections from Taiwan (Table 1, column 13).

There are abundant starch grains observed in the libriform fibers and ray parenchyma of ***P. moluccanum*** (fig. 17). In other species studied, no starch grain has been observed (Table 1, column 15).

2. Leaf characters:

Leaves of Formosan *Pittosporum* are glabrous. Only in *P. illicioides* var. *angustifolium*, multicellular trichomes are occasionally found (fig. 34). There are abundant druses in the cells of both palisade and spongy tissues (fig. 32). Among all species studied, *P. pentandrum* has the largest amount of druses. The subsidiary cells in Formosan *Pittosporum* are exclusively paracytic, as was described by Metcalfe and Chalk in Pittosporaceae as a whole (1950).

Some cells of the adaxial epidermis usually divide periclinally, thus 2-layered epidermis may be observed frequently (figs. 31-33), This is especially obvious in *P. pentandrum*, next clearest in *P. daphniphylloides*. Well-developed secretory canals have been obviously seen from transections, especially those sections through the midrib (fig. 33), in all leaves of Formosan *Pittosporum* (fig. 32).

Relations among component areas of internal structures of Formosan *Pittosporum* are presented in figure 1. It is apparent that *P. pentandrum* shows great diversities in these three measures, while these values are rather similar in *P. tobira*. Collections showing large diversities in these three percentages have more palisade tissue but less air space (i. e. the lowest three collections in figure 1). Among the collections of small diversities, lowland collections have more spongy tissue whereas alpine ones have less spongy tissue.

A positive correlation between the percentage of bundles sheath extension and the thickness of cuticle layer is shown in figure 3. Figure 3 also shows, that both the percentage of bundle sheath extension and the thickness of cuticle layers are scarce in relation to the area of palisade tissue; neverthless, within a single species, the larger the area of palisade tissue, the thicker the cuticle layer and the higher figure for the percentage of bundle sheath extension.

In collections with low figures for the vulnerability ratio, the area ratio of palisade tissue to air space also is low. *P. illicioides* and *P. illicioides* var. *angustifolium* have thinner cuticle, while in *P. tobira*, *P. moluccanum* and *P. daphniphylloides*, all have thicker cuticle.

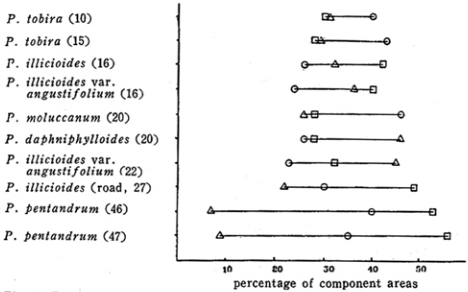

Fig. 1. Percentage relations of component areas among Formosan *Pittosporum*. The number in parenthesis indicates the distance between 2 terminal points; □: palisade tissue, ○: spongy tissue, △: intercellular space. (data from Table 2,)

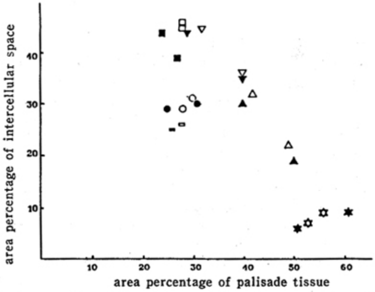

Fig. 2. Areas relationship between palisade tissue and intercellular space. (data from Table 2.)

□ : *Pittosporum daphniphylloides*
△ : *P. illicioides*
▽ : *P. illicioides* var. *angustifolium*
○ : *P. tobira*
✡ : *P. pentandrum*
▭ : *P. moluccanum*

(solid : mesophyll near petiole; empty : mesophyll near the maximum width)

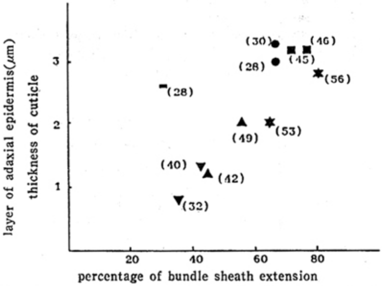

Fig. 3. Relations among the percentage of bundle sheath extension, the thickness of cuticle and the area of palisade tissue. (data from Table 2.)

✱ : *Pittosporum pentandrum*
■ : *P. daphniphylloides*
● : *P. tobira*
▬ : *P. moluccanum*
▲ : *P. illicioides*
▼ : *P. illicioides* var. *angustifolium*

(The number in the parenthesis indicates the percentage area of palisade tissue.)

DISCUSSION

1. Number of vessels per group:

The figures for vessels per group in most Pittosporaceae are low as has been reported by Carlquist (1981). If a low number of vessels per group is indicative of mesomorphy (Carlquist, 1966, 1975), Pittosporaceae could be said to be a basically mesic family (Carlquist, 1981), a generalization offered, in fact, by Schodde (1972). While all species of Formosan *Pittosporum*, except *P. daphniphylloides* which shows a great difference within two collections, the figures for different collections from a single species are rather close (Table 1, column 1). In *P. daphniphylloides*, it is reasonable to assume that the figure for collection from Chiti (roadside, 2.84) is higher than that from Alishan (mixed forest, 1.62). The figures for collection of *P. pentandrum* (1.80) from Henchuen Peninsula, a semi-open area, and for collection of *P. moluccanum* (1.88) from Island Lanyu, are rather close. Both localities are similar in climate and latitude. The long period of drought in the summer in Taipei area may account for the high figure (2.40) for *P. pentandrum* cultivated in National Taiwan University campus. Although the coastal plants are very drought-resistant, figures for both collections of *P. tobira* from northern Taiwan (2.45, 2.04) are lower than that for collection cultivated in Claremont, CA. (3.16 in Carlquist, 1981). This may be due to the usual rainy days along coast of northern and northwestern Taiwan. The diversity in number of vessels per groups seems to be influenced more by environment than by species differences.

2. Grwoth ring:

Generally speaking, growth rings may reflect the anatomical correlations of seasonal events. As shown in Table 1, column 14, the growth rings in alpine species are more conspicuous than those in lowland species. The growth ring in *P. pentandrum*, from Taiwan (figs. 7, 8) or cultivated in Claremont, is inconspicuous. In *P. tobira* and *P. moluccanum*, vessels are slightly wider in earlywood than in latewood (figs. 4, 13) but the growth ring activity is still inconspicuous. *P. tobira*, cultivated in Claremont, has been reported by Carlquist (1981) that vessels are wider and more numerous in early wood than in latewood. The differences of growth ring may be due to different climate and latitude. In Taiwan, the lowland is subtropical zone while the alpine area is temperate zones. In alpine species, vessels are wider and more numerous in earlywood than in latewood, thus the growth ring activity is more obvious (figs. 18, 19, 22, 23, 26, 29).

None of the growth rings in the Formosan alpine species show extreme differences between earlywood and Iatewood. It has been explained by Carlquist (1981) that "this circumstance may be related to the evergreen habit, whereby fluctuation in transpiration with respect to season is not as marked as in deciduous trees, which often have clearly marked earlywood with gigantic vessels, the definitive 'ring porous' condition of various authors". Besides, there is a long period of rainy days within May and June every year in Taiwan, and during this period, the rate of transpiration will be reduced and the diameter and number of vessel will decrease gradually.

3. Vessel diameter, vessel element length, vessel density, vulnerability ratio and mesomorphy ratio:

In Formosan *Pittosporum*, except for *P. pentandrum*, the vessel diameters are all less than 40 μm, while the average vessel diameter for Pittosporaceae as a whole is 42.2 um (Carlquist, 1981). Bass (1976) stressed a relationship between higher temperatures and greater vessel diameter. This holds true in wet tropics, but not in dry tropics or hot desert areas in various latitudes (Carlquist, 1981). ***P. pentandrum***, growing in subtropical and wet area, shows wider vessel diameter than other species. It has been recently hypothesized dy Carlquist (1980b) that species grown in tropical areas with abundant soil moisture and high temperatures results in almost constant transpiration of large volumes of water per unit time. One can understand why ***P. tobira***, in spite of growing in sunny and hot areas is pnovided with leathery evergreen leaves transpire water slowly but steadily throughout the year.

Air embolisms are usually formed within the vessel elements when the plant body is under drought or frost conditions. Slatyer (1967) avers, air embolisms within vessels do not spread the length of a vessel, but often tend to stop at the end wall (perforation plates). Carlquist (1982) hypothesized that shorter vessel elements, which better localize air embolisms would be advantageous to plants in dry habitats. It has been proposed by Carlquist (1982), in his study of Daphniphyllaceae, that under conditions where vessels are blocked by air embolisms, more numerous vessels are advantageous. Both vessel diameter and vessel density can be evolve more easily in contrast to vessel element length. Changes within a single growth ring in these respects can be seen readily. Vessel diameter and vessel density are independent of each other, within limits. Therefore they can be independent indications of mesomorphy and xeromorphy, and their independence justifies use of both measures in the construction of the "vulnerability" and"mesomorphy" ratios (Carlquist, 1981, 1982,).

Vulnerability values below 0.05 typify more xeric species in Pittosporaceae (Carlquist, 1981) as well as Daphniphyllaceae (Carlquist, 1982). "Xeric" release make deficits at temperatures above freezing and drought and physiological drought produced by freezing. In the genus ***Pittosporum*** studied by Carlquist (1981), the lowest values for the vulnerability ratio belong to the New Zealand alpine species, e.g. ***P. divaricatum*** (0.05) and ***P. turneri*** (0.09).

Figures for vessel diameter, vessel density, vessel element length, vuluerability ratio and mesomorphy ratio are given for Formosan ***Pittosporum*** in table 1, column 2,3,4,8, and 9, respectively. The figures for vessel density are rather high, but low for vessel element length, subsequently low for both ratios. Figures for vulnerability ratio for all collections are less than 0.5, thus they are indicative of xeromorphic species. Alpine species, e.g. ***P. daphniphylloides***, ***P. illicioides*** and ***P. illicioides*** var. ***angustifolium***, in spite of their growing under wet dense forest, have rather low figures for both ratios caused by winter frost, the same phenomena as those species in the New Zealand montane area. Collections of ***P. illicioides*** and ***P. illicioides*** var. ***angustifolium*** from the same locality have vulnerability ratios of the same value(0.11), and their mesomorphy ratios are also rather close (45; 48). In the two collections of ***P. tobira*** from the same coastal area, the figures of both species for the vulnerability ratio are 0.16 and the figures for mesomorphy ratio are 61. But there is some diversities for both ratios between the two collections of ***P. daphniphylloides*** from different regions. The difference in vulnerability ratios is obvious between the two collections of ***P. pentandrum*** from the NTU campus (0.46) and the Henchuen semi-open area (0.28). It becomes obvious that within a single species, no matter how the figures for both ratios vary, the variation is limited, and within this limitation, the figure is determined by the habitat. The range of habitat within a single species is also limited.

4. Helical sculpture on walls of vessel elements:

Helical sculpture has been found on walls of vessel elements for all species of Formosan ***Pittosporum*** except for *P. **pentandrum***. Helical thickenings were reported for the majority of genera in Pitforporaceae by Solereder (1908) and Metcalfe and Chalk (1950). Helical sculpture in vessels was found by Webber (1936) to be more abundant in vessels of desert shrubs than in those from more mesic regions. In Carlquist's study of Pittosporaceae (1981), the average figure for the mesomorphy ratio for the 27 collections having helical suclptures is 377, and the average figure for this ratio for the other 35 collections devoid of helical sculptures is 297. Jeje and Zimmermann (1979) have shown that there is a lessened resistance to flow in vessels which possess helical sculpture. Carlquist (1981) suggested that helical sculpture compensates for the lack of wider vessels. In the present study, only ***P. pentandrum*** has wider vessel diameter and is devoid of any helical thickenings on walls of vessel elements. All species except for ***P. pentandrum*** appear to agree with Carlquist's hypothesis (1981) that "selection disfavors wide vessels in such species". One could postulate that species growing under more xeric habitat tend to have narrow vessel diameters and helical thickenings on vessel element walls. Narrow vessels would prevent rapid water transpiration, but helical thickenings could decrease the resistance of water flow within the vessel elements. However the explanation for why spirals should have selective advantage in xeromorphs is unclear (Carlquist, 1975). There is no helical thickening on walls of vessel element in Formosan ***Pittosporum pentandrum***, but helical thickenings was found in ***P. pentandrum*** origined from the Philippines (Carlquist, 1981). This anatomical diversities seems to imply that Formosan ***Pittosporum pentandrum*** is subspecifically different from the Philippine's. Incidently Formosan ***P. pentandrum*** was once named as ***P. formosanum*** (Gowda. 1951; Kanehira,1936; Matsumura & Hayata, 1906).

5. Libriform fibers:

Metcalfe and Chalk (1950) generalize that Pittosporaceae as a whole is characterized by septate imperforate tracheary elements. All imperforate tracheary elements observed in the present study are libriform fibers, most of them are septate fibers. Among the 48 species of Pittosporaceae studied by Carlquist (1981), septate fibers are found in only 27 species, excluding ***P. tobira***. Obvious septate fibers are found in Formosan ***P. tobira*** (figs. 5a,b). This may be due to a regional variation. Kobayashi (1981) has proposed 6 species and 3 varieties with a new name or combination from ***Pittosporum tobira*** Ait. and its allied species. According to her criteria for classification, collections from Japan and S. Korea were ***P. tobira*** var. ***tobira***, whose inflorescences have rich long or both long and short, T-shaped hairs, and 6 to 10 flowers; collections from N.W. Formosa and S.E. China were accepted as ***P. tobira*** var. ***calvescens***, whose inflorescence have fewer T-shaped hairs,and 5 to 6 flowers. Based on morphological, anatomical and geographical evidence, a subspecies, i.e. ***P. tobira*** subsp. ***calvescens*** appears appropriate.

6. Wood parenchyma:

As has been reported by Carlquist (1981), narrow multiseriate rays or uniseriate rays are apparently correlated with the habit of New Caledonian and Hawaiian species with the 'distinctive growth form'. The narrow rays may correlate with the great strength of these pole like stem. Species that are freely branched shrubs or well-branched trees and shrubs, generally have wider rays. Among all collections in this study, the growth form of *P. illicioides* and *P. illicioides* var. *angustifolium*, growing under the same dense forest, are similar to the New Caledonian species; both collections have uniseriate rays (figs.25,28). *P. illicioides*, growing along roadsides in sunny places, grow into more or less well branched shrub, and on the other hand has more wide multiseriate rays (figs 30); on the other hand, if growing under wet dense forest, it will grow into a shrub with numerous slender branches, thus has more uniseriate rays and narrow multiseriate rays.

The rays in Formosan *Pittosporum* correspond to the Type Kribs (1935) called Heterogeneous Type IIA, as Carlquist (1981) has reported for Pittosporaceae as a whole. But Metcalfe and Chalk (1950) interpret these rays in Pittosporaceae as Heterogeneous IIB or Heterogenous I.

7. Leaf anatomy and its ecological implication:

Patterns in the variation of internal leaf structure generally correlate with environment have been known for a long time. Xeromorphic leaves usually have thicker leaves, cuticles, palisade tissues. The multi-layered epidermis is also frequently found in xeromorphic leaves (Esau 1965, 1977; Tsai, 1984). The internal leaf structure of Formosan *Pittosporum*, possesses one or more xeromorphic characters. *P. daphniphyll-oides* has a thick leaf blades and thick cuticle layers, but lower percentage of palisade tissues; occasionally 2-layered adaxial epidermis are observed. *P. pentandrum* has a greater palisade thickness than other Formosan *Pittosporum*, frequently 2-layered adaxial epidermis are found, but in such cases the cuticle and blade are not as thick as those of *P. daphniphylloides*. Both *P. illicioides* and *P. ilicioides* var. *angustifolium* have medium palisade tissue but thinner leaf blades. These suggest that the leaves of Formosan *Pittosporum* are mesomorphic, but with some tendency toward xeromorphic.

Jackson (1967) studied the effect of shade on leaf structure and found that blade thickness was reduced by shade, however reduction in the development of spongy mesophyll under shade was apparently much less than that of the palisade tissue. The ratio between the internal free surface area of the leaf and its external surface is small in shade leaves (6.8 to 9.9), medium in mesomorphic leaves (11.6 to 19.2) and large (17.2 to 31.3) in xeromorphic leaves (Turrell, 1936). A high figure for this ratio is xeromorphic leaves was reported due to that, in unit volume the surface area of palisade is about 1.6 to 3.5 times as the surface area of spongy tissue (Turrell, 1939). In Turrrell's (1944) further study of the effect of light intensity on both xeromorphic leaves ((*Nerium oleander*) and mesomorphic leaves (*Vinca rosea*), he found both types were influenced by light intensity. A certain degree of xeromorphy could be induced in both types under high intensity. Comparing the three percentages of internal component areas, i.e. palisade tissue, spongy tissue and air space, of leaves in Formosan *Pittosporum* (fig.1), collections of *P. pentandrum* from two localities and *P. illicioides* from roadside, all are under sunny area, show more palisade tissue and less air space, the xeric characters induced by light intensity. As mentioned before, among the collections of medium diversities in these three area percentages, lowland collections have more spongy mesophyll while alpine ones have less spongy tissue but more air space. This may be concerned with the fact that the air is thinner in montane areas than in lowland areas, thus much amount of air is needed to be fixed within the leaves for alpine species.

Bundle sheath extensions are generally observed along the veins in leaves of Formosan ***Pittosporum***. Wylie (1952), in his study at leaves of 348 dicotyledon species from three separate regions, reported that 210 possessed bundle sheath extensions. He also noted that species devoid of bundle sheath extensions have greater blade thickness cuticle thickness, adaxial and abaxial epidermal cells, palisade mesophyll and spongy mesophyll than species with bundle sheath extension. In present study, however only a positive correlation between thickness of cuticle layer and percentage of bundlesheath extension can be detected (fig. 3). Although there is no direct relationship between palisade area and cuticle thickness or percentage of bundle sheath extension, within a single species, the larger the area of palisade mesophyll, the higher the figure for percentage of bundle sheath extension. There is proof that the bundle sheath extension have a same conduction function as veins in the leaf (i.e. Wylie, 1943). They conduct from the bundles to the epidermal cells. The ratio of palisade tissue to spongy tissue is closely related to vein spacing : the greater this ratio, the closer is the spacing (Esaü, 1977; Fahn, 1952, 1982; Wylie, 1952). As mentioned above, variation of internal leaf sturcture is determined by environment. It is also shown from the present study, that, in leaves with thick palisade tissue, more bundle sheath extensions and more veins are present. The thick cuticle on leaves with high percentage of bundle sheath extensions may prevent water transpiration through the bundle sheath extensions.

Among the species with lower figures for vulnerability ratios, only ***P. daphniphylloides***, ***P. moluccanum*** and ***P. tobira*** have thick cuticle layers. This means these three species possess more xeric character than the other two species, ***P. illicioides*** and ***P. illicioides*** var ***angustifolium***, which also have lower vulnerability ratio. All above, the latter two have these figures lower than those of the former three. The low figure for this ratio for ***P. illicioides*** and ***P. illicioides*** var. ***angustifolium***, in spite of their thin cuticle layers and low value for ratio of palisade tissue to air space, is mainly due to physiological drought, caused by the winter frost. The low figure for the vulnerability ratio for ***P. daphniphylloides*** reflects a form of thick cuticle layers and physiogical drought. As for the lowland species, with more thick cuticle, i.e. ***P. moluccanum***, ***P. tobira***, or even with higher value for ratio of palisade tissue to air space, the low figure for both vulnerability ratio and mesomorphy ratio may be caused by high temperatures, and the sunny weather and long period of drought in summer.

When the area percentage of intercellular space, spongy tissue and palisade tissue are compared in pairs, there is somewhat a negative correlation between the areas of space and palisade tissue as shown in figure 2. Collections from the similar habitat may be grouped together and separate from other groups. As shown in figure 2, the ***P. illicioides***, growing along the roadside at medium altitude, is in mid course between lowland ***P. pentandrum*** and dense-forest, high altitude of ***P. illicioides*** and ***P. illicioides*** var. ***angustifolium***.

In Formosan ***Pittosporum***, each species possesses a habitat with a limited range, and within this range, the anatomical characters of leaves and stems vary in a limited range. Different species growing close together or under similar environments, have similar anatomical characteristics.

ACKNOWLEDGEMENT

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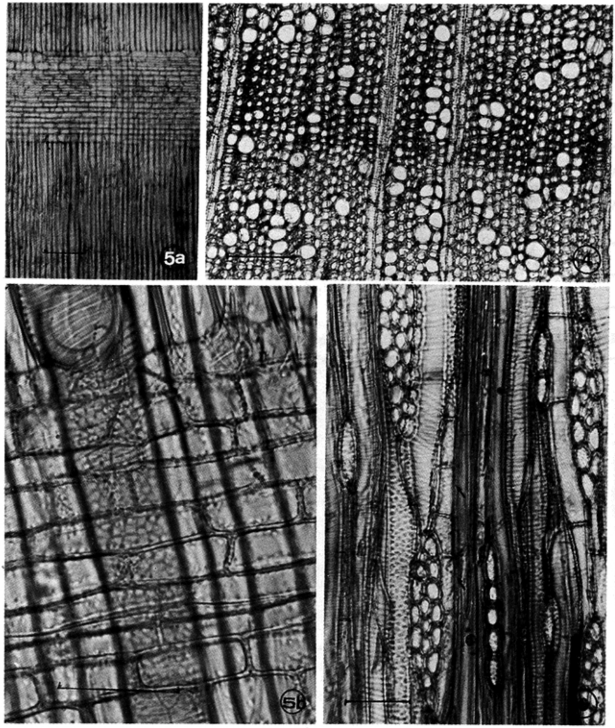
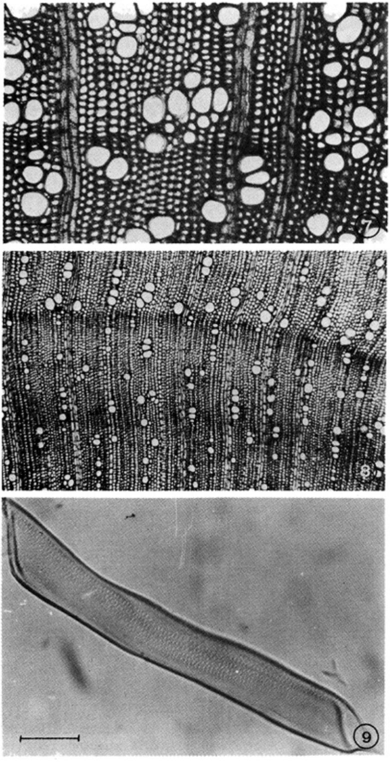
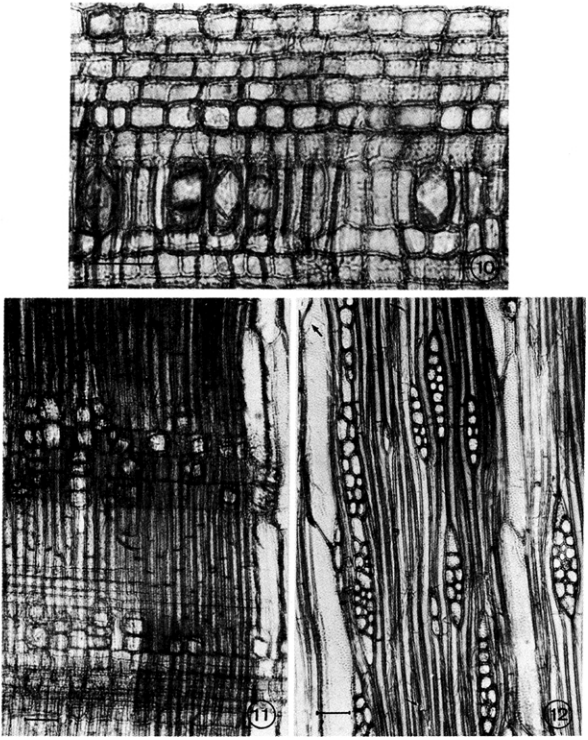


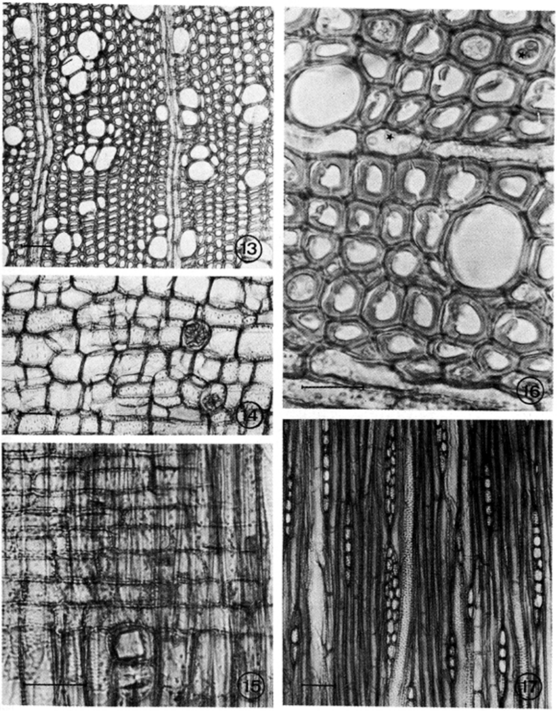
Figures 4-6. Wood sections of *Pittosporum tobira*. 4. Transection, showing moderate vessels; moderate growing ring activity evident. 5. Radial section, rhomboidal crystal wanting, vessel with simple perforation plate, helical sculpture and alternate pitting. 6. Tangential section rays mostly multiseriate with 2—3-celled in width; libriform fibers obviously septate; scanty paratracheal axile parenchyma observed (arrows indicated); vessels with alternate pitting and helical sculpture. scale 100 μm for 4,5a; 50 μm for 5b,6.



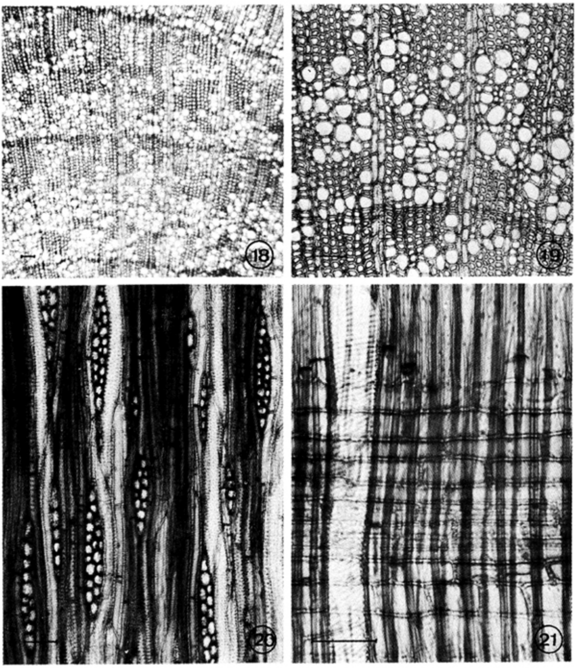
Figures 7-9. Wood sections of *Pittosporum pentandrum* 7. Transection, moderate vessels, the growth ring activity is less evident. 8. Transection, in lower magnification, the vessel groupings arrange in more radial direction. Figure 9. Macerated vessel element of *P. pentandrum*. Alternate pitting, devoid of helical sculpture. scale 50 μm.



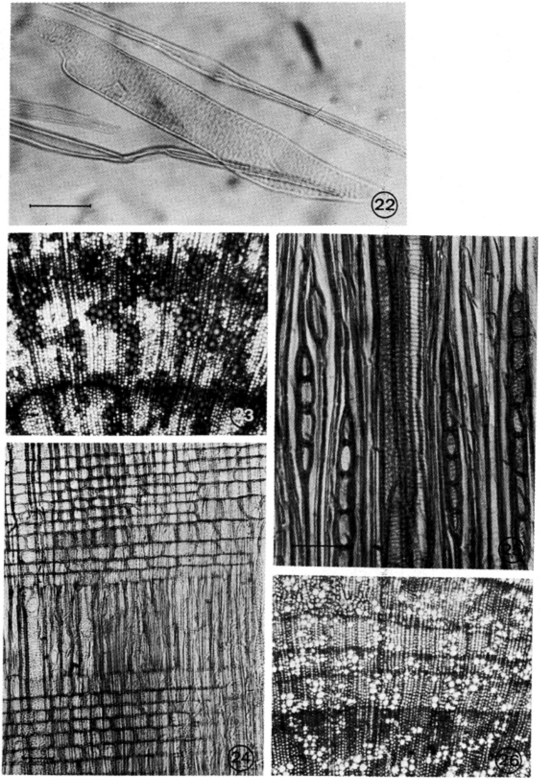
Figures 10-12. Wood sections of *Pittosporum pentandrum*, 10. Radial section, showing large rhomboidal crystals in erect wing cells, in some case, in the subdivided wing cells. 11.. Radial section; much rhomboidal crystals present in erect ray cells and subdivided wing cells. 12. Tangential section, showing vessels with simple perforation plate (arrow indicated) and alternate pitting; septate fibers observed. scale 50 μm.



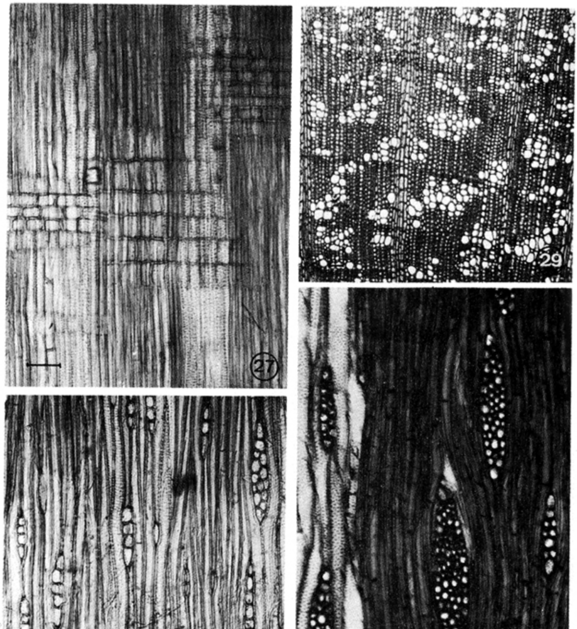
Figures 13-17. Wood sections of *Pittosporum moluccanum*. 13. Transection, vessels in moderate number, the growth ring activity is less evident. 14. Radial section, druses from pith cells. 15. Radial section, subdivided wing cell contains crystals; rays heterogeneous type, the dark stained particles seem to be starch grains. 16. Transection in high magnification; simple pits in libriform fiber clearly observed; starch grains present in both ray parenchyma and libriform fibers (stars labelled). 17. Tangential section, narrow multi-seriate rays and much uniseriate rays; septate fibers also be observed. scale 50 μm for 13-15, 17; 25 μm for 16.



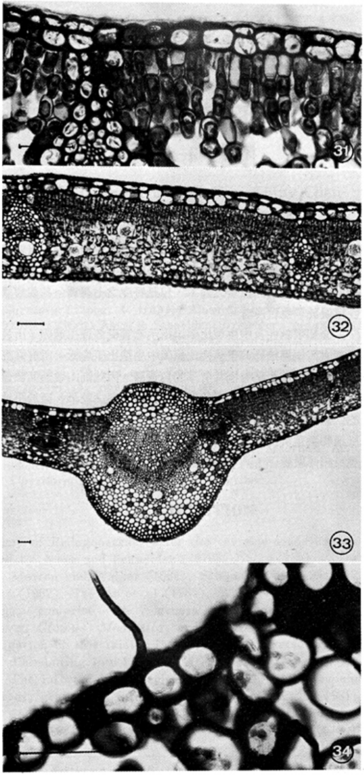
Figures 18-21. Wood sections of *Pittosporum daphniphyllloides*. 18-19. Radial sections, showing numerous vessels with growth ring activity evident, the vessels in early wood is both wider and more numerous than in latewood. 20. Tangential section, vessels with alternate pitting and helical sculpture present; narrow multiseriate rays noted, septate fibers also observed. 21. Radial section, square wing cells and radial elongated body cells are seen; none of crystals observed; vessels with helical sculpture and simple perforation plate noted. scale 50 μm.



Figures 22-26. Wood sections of *Pittosporum illicioides* (in dense forest). 22. Macerated wood element showing helical sculpture. 23. Transections, the growth ring activity is evident, the vessels, not only wider in early wood but also more numerous in eatly wood than in late wood, the radial patches of vessel grouping are conspicuous. 24. Radial section,none of crystals observed, the procumbent ray cells are less radial elongated. 25. Tangential section, rays are tall but narrow, uniseriate abundant. Figure 26. Wood transection of *P. illicioides* var. *angustifolium*. The growth ring activity is also evident, the radial and diagonal patches of vessel groupings are somewhat evident. scale 50 μm.



Figures 27-30. Wood sections of *Pittosporum illicioides* var. *angustifolium*. 27. Radial section, rhomboidal crystal in the upright ray cell, the body cells are less radial elongated as seen in fig. 24. 28. Tangential section, showing more uniseriate rays. Figures 29-30. Wood sections of *P. illicioides* (in roadside). 29. Transection, the growth ring activity evident, the diagonal and tangential patches of vessel grouping conspicuous. 30. Tangential section, the wider multiseiate rays are more abundant than in fig. 25. scale 50 μm.



Figures 31-34. Transections of leaves. 31. *P. daphniphylloides*. 2-layered epidermis with distinct nucleus within each were observed. 32. *P. pentandrum*. Druses observed in both palisade and spongy mesophyll. 33. *P. pentandrum*. Near the petiole, the midrib showing an arc-shaped of vascular tissue; also note the 2-layered epidermis. 34. *P. illicioides* var *angustifolium*, multi-cellular trichome on adaxial surface. scale 50 μm.

臺灣海桐屬莖葉之解剖研究在生態上之含義

陳麗霞 黃增泉

摘要

海桐科僅分布於舊世界，臺灣則僅產海桐屬，包括五種及一變種。分布自低海拔（海桐、七里香及蘭嶼海桐）經中海拔（部分疏果海桐）至高海拔（疏果海桐、細葉海桐及大葉海桐）。其中僅栽培之七里香，可成爲小喬木者，餘爲或高或矮之灌木，包括野生之七里香。於生育習性上，臺灣之海桐屬植物，均屬中生習性稍偏於旱生習性者。

Carlquist（1977）介紹爭執性及中生型比值以指示導管受各種生態因子所發生反映情況。就整個海桐科植物而言，臺灣之海桐屬植物其爭執性比值與中生型比值均低。所有之高山種類均具有低的柵狀組織對細胞間隙之比值，但僅大葉海桐具有厚的角質層。因此高山種類低數值的爭執性與中生型比值，主要源於冬季高山常有凍霜之現象，因此引起植物體生理之乾旱。至於平地種類多具較厚之角質層，而此兩種比值的低數值，則起因於高溫，强光照及夏季常有長期乾旱的結果。

研究臺灣產海桐屬植物葉莖解剖性質而獲得結論卽同種海桐植物生於不同環境下，解剖性質不同，而不同種海桐植物生於相同環境下，具有類似解剖性質。