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The Vessel Member of Myrica esculenta Buch.-Ham.

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ABSTRACT — The vessel members of *Myrica esculenta* from two trees, one in Sarawak, the other in Singapore, are described. The differences in habitat as well as in vertical position in each tree have a minor influence on dimensional characteristics of the vessel members. However, radial position is very significant. Average length of element increases from 600μ to 950μ between .05 cm from the pith to 1.75 cm from the pith and then ceases to elongate appreciably. Average diameter over the same radial distance increases from 30μ to 105μ. Also over the same radial distance, the average number of perforations of the end-wall decreases from 16 to 7 and the average end-wall angle increases from 14° to 42°. In these respects *Myrica esculenta* has primitive to intermediate vessel members. The data provide a basis for evaluation of the evolutionary status of the other species of the *Myricaceae* which are available to us only in the form of fragmentary wood specimens.

A world-wide study of the wood structure of numerous members of each of the recognized genera of the *Myricaceae*, or Bayberry Family, is part of a combined approach using various characters for a reappraisal of the relationships of the family among *Dicotyledonae* and within the *Myricaceae*. The present paper uses the tree species *Myrica esculenta* to compare variation in length, diameter, end-wall angle and number of perforations per end-wall of the xylem vessel member as related to radial and vertical position in the stem. It is anticipated that this will subsequently lead to a better understanding of vessel member specialization among different species within the *Myricaceae*.

The Bayberry family includes 56 or more species of Eurasia, Africa, the Americas and adjacent islands as well as one species on New Caledonia in the South Pacific. The species vary in habit from the fifty- to sixty-foot trees of the tropics to the slender-branched shrubs of the subarctic and South Africa. Most species are shrubs often preferring moist to swampy habitats.

Engler and Prantl (1897), Rendle (1925), Hjelmquist (1948) and others have placed the *Myricaceae* among the so-called catkin-bearing *Amentiferae*, which they thought to be primitive flowering plants because of what they considered to be simple flowers and flower clusters or inflorescences. Many of the families which they characterized as having "aments" or "catkins" have upon more careful examination proven to be anything but simple axes bearing a single, unstalked or sessile floret at each node forcing systematists such as Lawrence (1951) who follow Engler's classification to redefine the terms *ament* and *catkin*. For these and other reasons Bessey (1897), Hutchinson (1926), Tippo (1942) and others consider the "Amentiferae" to be an artificial assemblage of families with various taxonomic affinities, and varying degress of specialization.

Since the publication of the classical papers of Bailey and Tupper in 1918, and of Frost in 1930-31, the value of secondary wood or xylem and especially of the vessel member for providing evidence of the ancestry and relationships of woody plants has been firmly established (Metcalfe and Chalk, 1957). Bailey and Tupper measured large numbers of water-conducting or tracheary cells from 160 species representing 42 genera which included all major groups of *Gymnospermae* and over 240 species from almost as many genera representing 180 of the families of *Dicotyledoneae*. The work of these and of other anatomists permits certain generalizations to be made concerning phyletic sequences in regard to vessel member specialization (see Table 1).

Vessel members of the late wood of the *Myricaceae* vary from 300-1,450 micra long, with the means generally less than 1,000 micra. Vessel member diameters vary from 15-225 micra with means generally less than 100 micra. Vessel member end-wall angles vary from 0°-80° with reference to the long axis of the cell but most end-wall angles are in the 20°-40° range. The number of mostly scalariform perforations per vessel member end-wall varies from 1 through 25, with most species examined falling within the 5-15 range per end-wall. Width of perforations may vary greatly at the two ends of the same vesel member as may the number of perforations and the end-wall angle. Vessel member pitting approaches scalariform or ladderlike at one extreme; at the other extreme there are opposite, transverse to almost alternate pit arrangements. Pitting is generally opposite. Vessel arrangement, as seen in cross section, is diffuse in most cases but may be very slightly clustered or slightly ring porous in temperate species. These is no evidence of storied arrangement as seen in radial or tangential sections for very advanced woods. On the basis of our preliminary survey of various species of the *Myricaceae*, confirming and extending the data found in Metcalfe and Chalk's encyclopedic survey of plant anatomy, it appears that *Myricaceae* vessels range from upper primitive to intermediate types.

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TABLE 1. Vessel member characters usually associated with primitive, intermediate, advanced, or very advanced families of the woody *Dicotyledoneae.*

Vessel Member	Primitive	Intermediate	Advanced	Very Advanced
Absent or present	absent to present	present	prsent to lost	- - - - - - - - -
Mean length in micra	1,900–800	800–350	350–175	- - - - - - - - - -
Mean diameter in micra	25–100	100–200	200–400+	- - - - - - - - - -
Mean end-wall angle in degrees	5–30	30–80	80–90	- - - - - - - - - -
Mean number of perforations per end-wall	16+	16–6	6–1	1
Outline in cross-section	angular	angular to round	round to oval	- - - - - - - - -
Mean wall thickness in micra	2.5 or less	2.5 to 4 or more	- - - - - - - - -	- - - - - - - - -
Intervascular and parenchyma/ vessel pitting	scalariform to transitional scalariform to opposite	transitional scalariform to opposite to mixed opposite and alternate	alternate	- - - - - - - - - -
Vessel arrangement in cross-section	diffuse-porous	tending to occur in clusters, or in temperate species, ring porous		
Tracheary elements storied	no	no	no	yes

Table 2 reveals a further complication in the interpretation of those characters related to vessel size. The lengths of the first-formed secondary xylem vessel members next the pith are considerably less than of those formed farther from the pith. Bailey found that this was because the cambial initials, which produce new vessel members, tracheids, fibers, etc., are themselves becoming longer during the first 5 to 30 years of growth of a woody stem. The length of time required for reaching maximum length of cambial initials varies with each species of woody plant whether Dicot or Gymnosperm. The only exceptions seem to occur among the most advanced dicot woods with storied cambium in which vessel length remains constant in the early and late wood. In addition, vessel cells tend to repeat their phylogenetic history by becoming relatively wider as new wood is added. Similarly, the end walls become less oblique and the number of scalariform perforations becomes less until the late wood is reached.

In order to study the maximal range of variation within a single species of the *Myricaceae*, a tree species, *Myrica esculenta*, was chosen for intensive study. Wood specimens were obtained from throughout its geographic range from Java to the Himalayas and southeast China, around the South China Sea, a region noted for the less specialized representatives of various dicot families. The data presented in this paper are based on systematic collections of wood samples from two typical trees, one on the island of Singapore and the other near Kuching in Sarawak, on the island of Borneo. These trees were felled and cross-sections taken from straight-grained mid-internodal wood of the main trunk at regular intervals from one foot above the ground to the top of each tree. From each cross-section samples were taken from wood near the pith, and from mature wood near the cambium. For larger cross-sections an additional sample was taken halfway between pith and cambium. Two cross-sections, one near the base of each tree was sampled continuously from close to the pith to the latest formed mature wood next the cambium. Sections were made in three planes and stained with safranin and fast green and representative samples were macerated with Jeffrey's fluid, stained with 1% safranin, dehydrated in alcohol and mounted in Harleco Resin dissolved in xylol.

TABLE 2. Comparison of mean lengths of early- and late-formed vessel members (*i.e.*, close to and far from the pith respectively) in woody *Dicotyledoneae.*

	Early	Late
Dicots with primitive secondary xylem vessel members	710 micra	1,100 micra
Dicots with transitional secondary vessel members	360 micra	730 micra
Dicots with highly specialized vessel members	260 micra	400 micra
Dicots with high specialized vessel members and storied cambium, etc.	170 micra	170 micra

The results of measuring length, diameter and end-wall angle and counting scalariform end-wall perforations for some 2400 vessel members from the two trees of *Myrica esculenta* just mentioned are summarized in four graphs on which the scale for each character used is recorded on the ordinate and the distance from the pith is recorded on the abscissa. Each point is an average for 35 or more vessels. The two trees are indicated by the thin and thick circles respectively and height above ground from which the samples were taken is indicated by a number starting with 1 at 1 foot above ground. It will be noted that distance above ground does not affect any of the four vessel member characters.

The graph for length of element plotted against distance from the pith shows an increase in average vessel member length from 600 to over 950 micra (over 150%) between .05 cm and 1.75 cm average distance from the pith. Beyond 1.75 cm from the pith average vessel member length has reached its upper asymptote. For average diameter plotted against average distance from the pith,

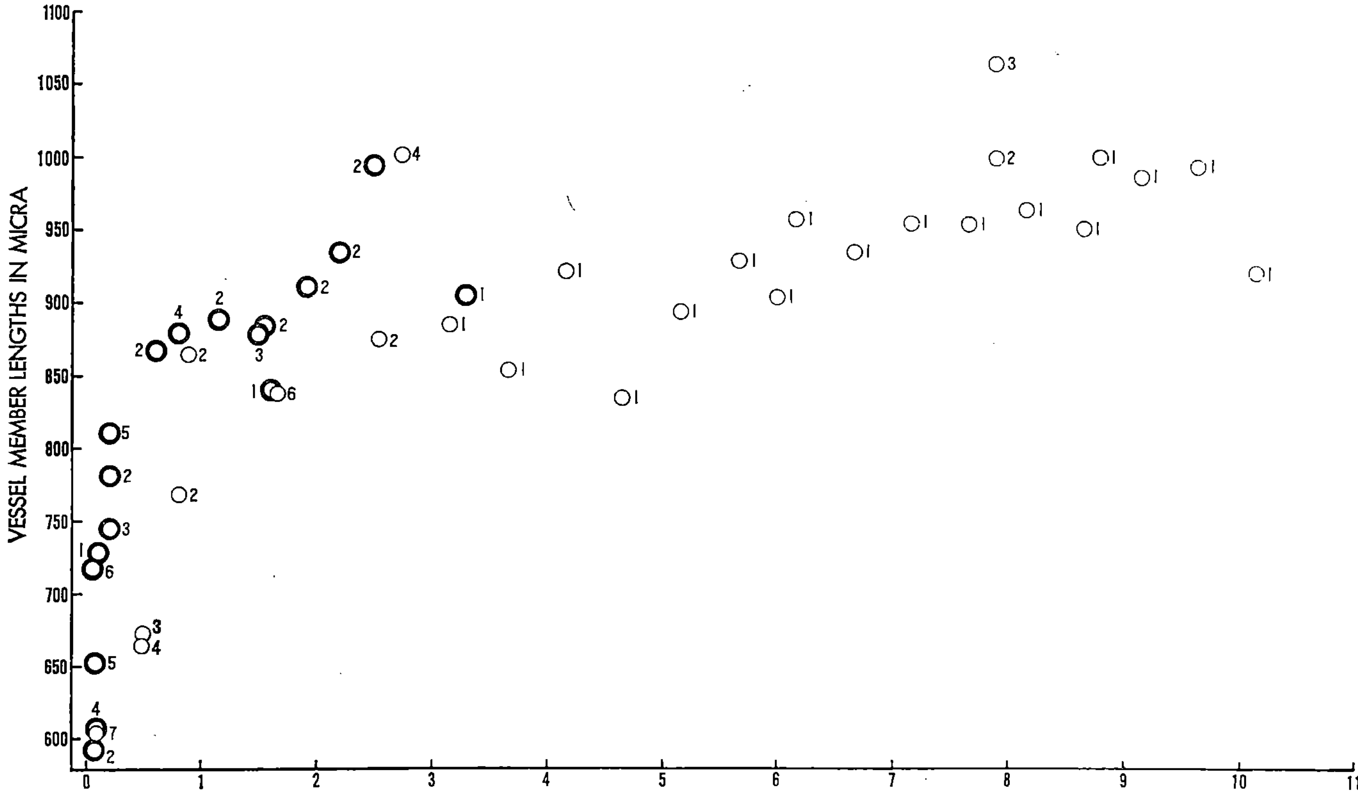
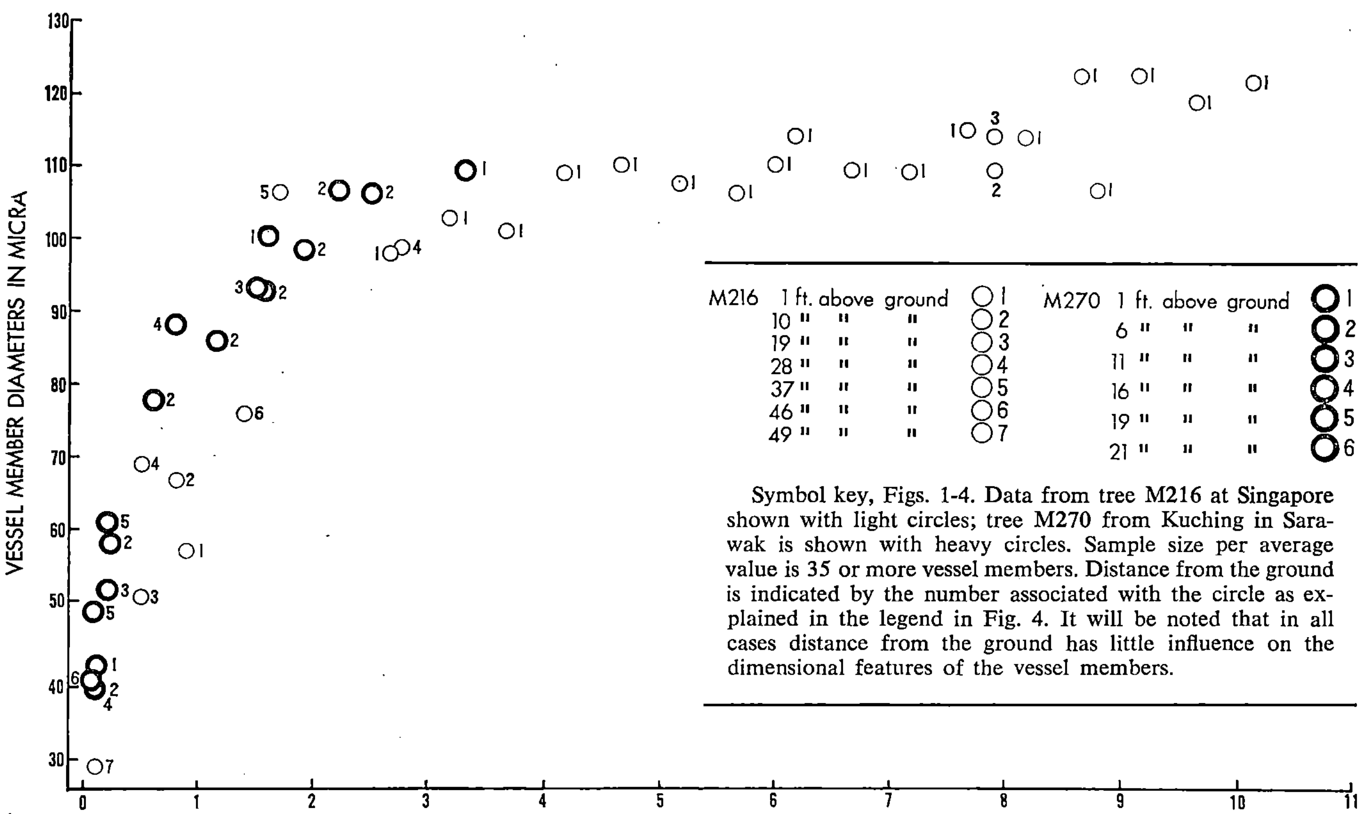


Figure 1 — DISTANCE FROM THE PITH IN CENTIMETERS

between .05 cm and 1.75 cm from the pith, average diameter increases from less than 30 micra to more than 105 micra (a more than 300% increase). Beyond 1.75 cm, diameter levels off at approximately 110 micra. Comparing increase in diameter and length between .05 and 1.75 cm one sees that the ratio of diameter over length



Symbol key, Figs. 1-4. Data from tree M216 at Singapore shown with light circles; tree M270 from Kuching in Sarawak is shown with heavy circles. Sample size per average value is 35 or more vessel members. Distance from the ground is indicated by the number associated with the circle as explained in the legend in Fig. 4. It will be noted that in all cases distance from the ground has little influence on the dimensional features of the vessel members.

Figure 2 — DISTANCE FROM THE PITH IN CENTIMETERS

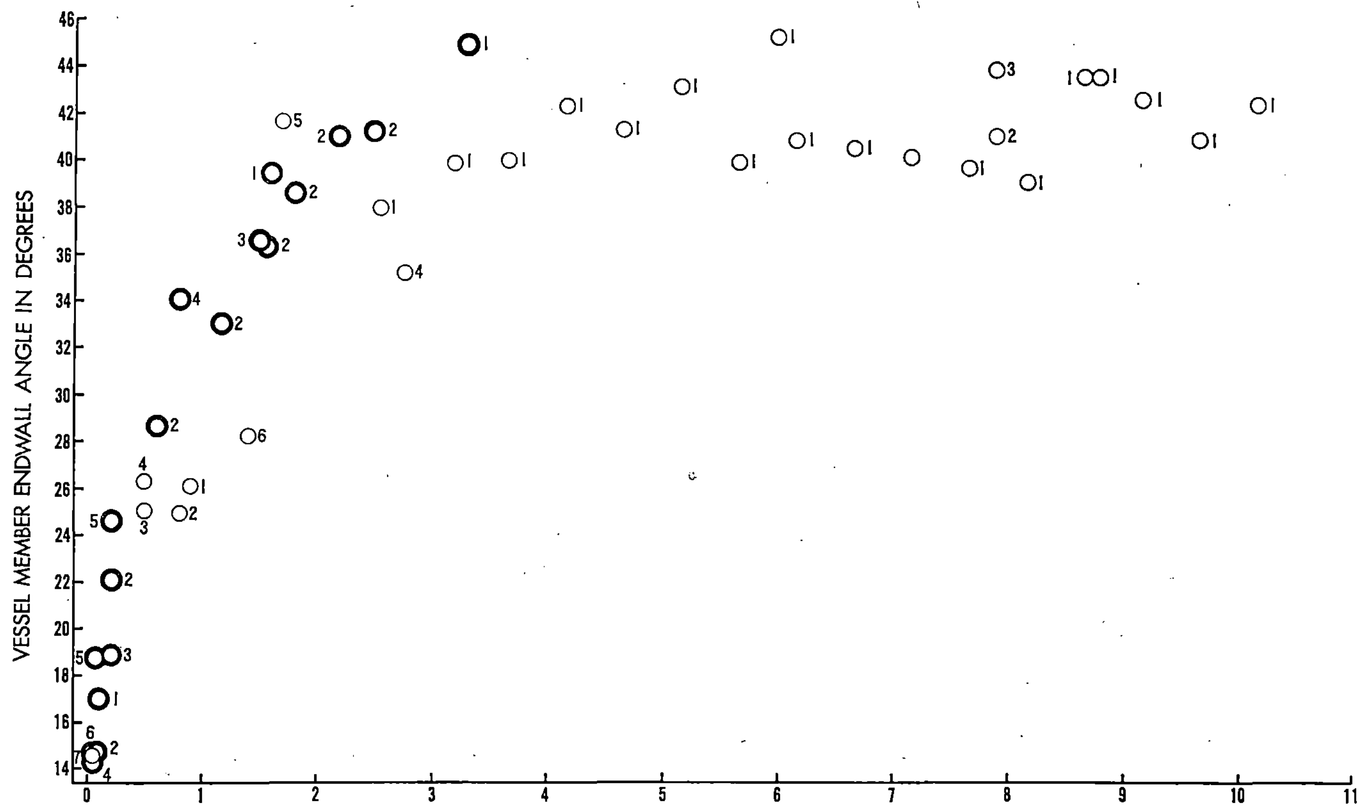


Figure 3 — DISTANCE FROM THE PITH IN CENTIMETERS

increases from 1/20 to slightly more than 1/10. Average end-wall angle increases from slightly over 14° at .05 cm from the pith to almost 42° at 1.75 cm from the pith after which it levels off at less than 44°. Since number of scalariform perforations tends to *decrease* as vessel diameter and end-wall angle *increase,* average number of

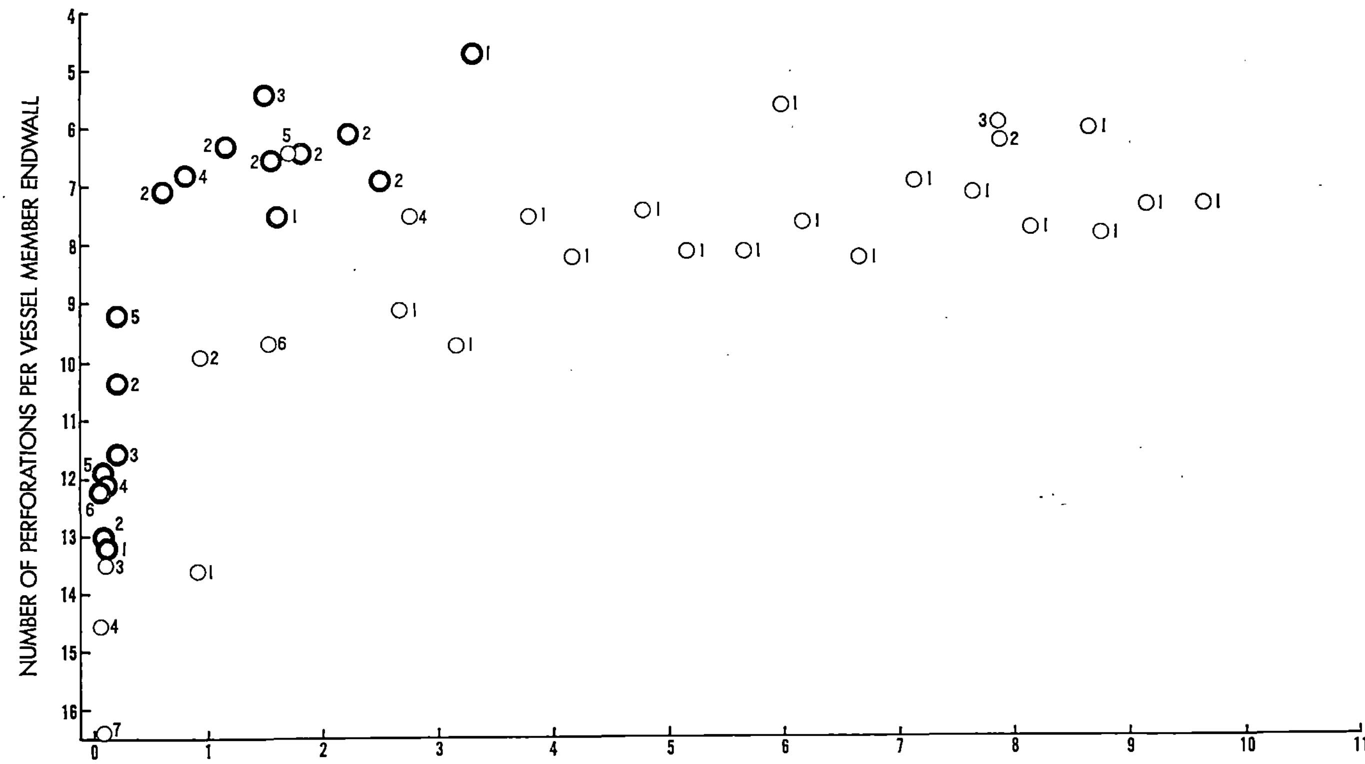


Figure 4 — DISTANCE FROM THE PITH IN CENTIMETERS

perforations are recorded on the abscissa with the highest number at the bottom and the lowest number at the top. From an average number of 16 perforations at an average distance of .05 cm from the pith the average number of perforations decreases to about 7 at an average of 1.75 cm from the pith after which average number of vessel member end-wall perforations levels off. (See Figs. 1-4).

It is evident then that vessel member length increases as mature vessel members are added to those of the first secondary wood between .05 and 1.75 cm from the pith. In the same region the ratio of diameter to length increases. Mature vessel member end-wall angles have tilted toward the transverse plane apparently in response to increase in diameter. Number of end-wall perforations decreases. It will now be seen how knowledge of the average variation in vessel member length, diameter, end-wall angle and number of perforations per end-wall can be used to evaluate the degree of specialization of vessels of other *Myricaceae* as compared with those of *Myrica esculenta.* For example the shrubby *Comptonia peregrina* (L.) Coult., or Sweet Fern, of Minnesota and the northeastern United States has a large proportion of secondary xylem vessel members with only a single perforation in the end-wall close to the pith, a type found only rarely in late wood of *Myrica esculenta.* On the other hand the shrubby *Myrica cerifera* L. of the eastern United States has much the same vessel member variation as *Myrica esculenta,* indicating an only slightly more specialized vessel since most of the wood examined was less than 1.75 cm from the pith. Both species have noticeably less specialized secondary xylem vessel members than Sweet Fern. *Myrica Gale* L., or *Gale palustris* (Lam.) Chev., has xylem characters which rather closely resemble those of *Myrica esculenta* secondary wood very close to the pith and primary wood. Thus although it should undoubtedly be considered specialized on the basis of reduction in plant size its vessel specialization might be considered quite comparable to that of *Myrica esculenta* rather than less specialized as might at first appear to be the case.

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