OBSERVATIONS ON THE LIGULATE TIP

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ABSTRACT

Statistical analyses were used to categorize interactions among morphological characteristics of ligulate tips and other characteristics of vessel elements. The results indicate that the ligulate tip is an evolutionary artifact. The phylogenetic specialization of ring porous genera has resulted in mucronate tips with minor overlap.

Keywords: Ligulate tip, vessel element, vessel arrangement.

INTRODUCTION

The ligulate tip, a tapering extension of vessel elements beyond the perforation that results in an overlap of adjacent vessel elements, is a well-known morphological structure. It is a common characteristic of vessel elements in hardwood genera. Variations in this structure sometimes serve to identify species. However, the ligulate tip's significance in phylogenetic research has not been reported.

METHODS AND MATERIALS

Morphological characteristics of vessel elements of twenty-seven genera common to North America were categorized from photographs and descriptions reported in scientific references (Carpenter et al. 1963; Panshin and DeZeeuw 1980; Parham and Gray 1982). The characteristics categorized were:

1. *Pore arrangement*—ring porous, semi-ring porous, diffuse porous.
2. *Perforation type*—simple, scalariform or foraminate, both simple and scalariform or foraminate.
3. *Ligulate tip shape*—mucronate (terminates abruptly), attenuate (tapers gradually), both mucronate and attenuate.
4. *Ligulate tip overlap*—major (as in *Liriodendron*, Fig. 1), minor (as in *Quercus*, Fig. 2), both major and minor.

Since these four characteristics were qualitative rather than quantitative, the data were divided into groups. The groups were analyzed by chi-square statistical analysis (Steele and Torrie 1960).

RESULTS AND DISCUSSION

The vessel characteristics assigned to genera are reported in Table 1. The data are adequate to permit statistical evaluation of the relationships of characteristics even though there are variations among species within genera, among plants within species, and among sampling locations within plant stems. Because of such variation, and the fact that descriptions and photographs were not available for all species in every genus, the information is not complete.

Vessel characteristics with the probabilities for the distributions predicted by

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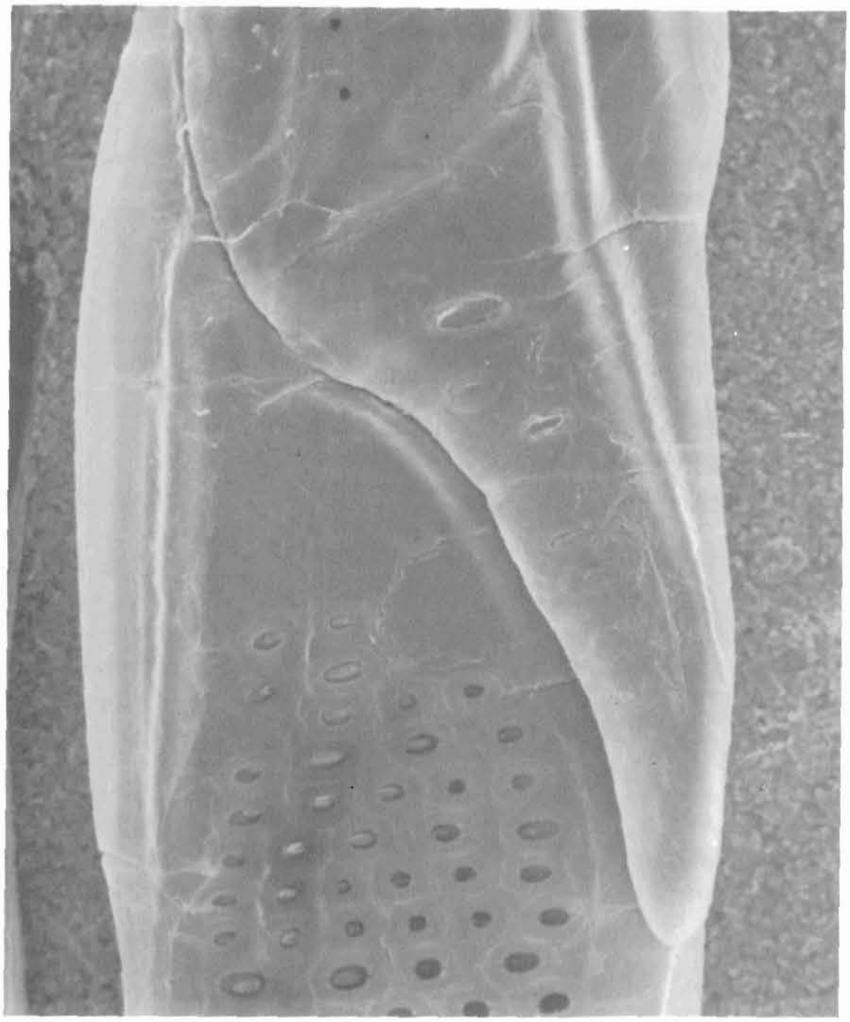

FIG. 1. Micrograph of an attenuatic ligulate tip showing a major overlap of a vessel segment of *Liriodendron tulipifera* L.

chi-square are reported in Table 2. Relationships between single vessel characteristics proved more significant than relationships between multiple characteristics. Because of the nature of the chi-square statistical analysis, the interactions between multiple vessel characteristics are not significant and are not reported in Table 2.

The relationship between vessel arrangement and perforation type had a probability of 0.109. This value indicates that ring porous genera and semi-ring porous genera have simple perforations, but diffuse porous genera have either simple or scalariform perforations. This relationship was reported by Gilbert (1940), who concluded that ring porosity is an advanced feature of angiosperms.

Approximately half of the genera evaluated have both mucronate and attenuate ligulate tip extensions. However, genera that are ring porous and semi-ring porous tend to have mucronate extensions (chi-square probability 0.042). In genera with

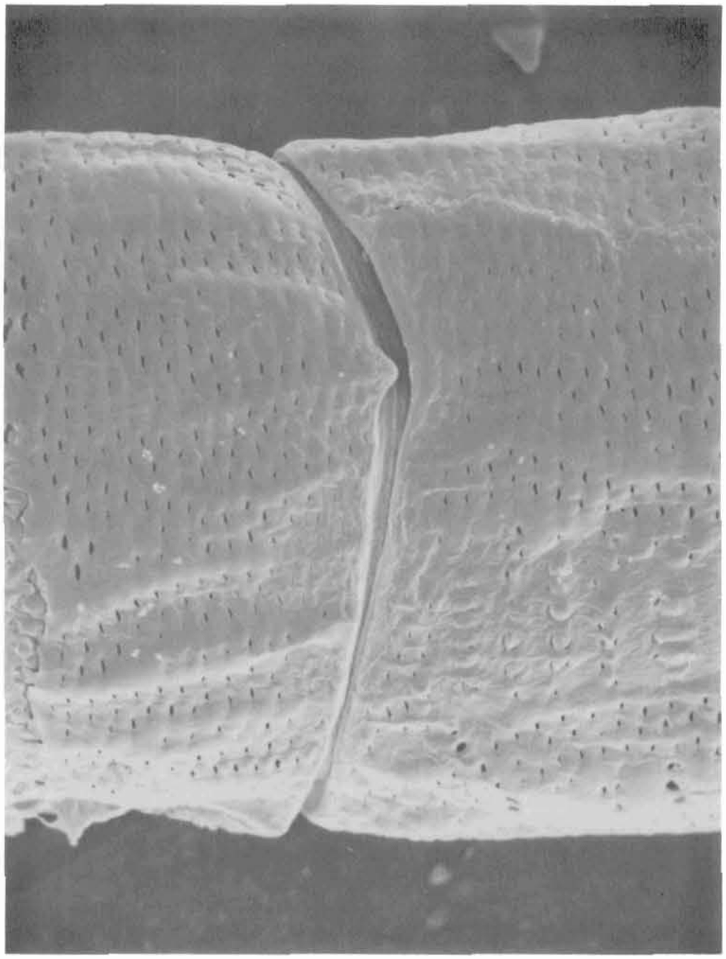

FIG. 2. Micrograph showing a mucronate ligulate tip with a minor overlap of a vessel segment of *Quercus nigra* L.

both types of ligulate tips, springwood vessels are mucronate, and summerwood vessels are both mucronate and attenuate.

The relationship between perforation type and ligulate tip shape (chi-square probability 0.017) indicates that genera with simple perforations have mucronate tips and genera with scalariform perforations and *Magnolia* have attenuate tips. Again, note that approximately half of the genera have both tip shapes.

Ligulate tip shape is, then, related to both pore arrangement and perforation type. The relationship of these vessel-element morphological characteristics is attributed, in part, to growth variations and ontogeny. For example, excessive lateral enlargement of vessel members during ontogenetic maturation leads, at times, to the formation of transversely oriented scalariform perforation plates, and the retardation of such lateral expansion may result in retention of tapered ends by short vessel members (Bailey 1944).

Frost (1930) shows that the inclination of the vessel end wall changes from the

TABLE 1. *Predominant vessel characteristics for selected genera.*

Genera	Pore arrangement[a]	Perforation type[b]	Ligulate tip shape[c]	Ligulate tip overlap[d]
Acer spp.	3	1	3	3
Aesculus spp.	3	1	1	3
Alnus rubra	3	2	3	3
Betula spp.	3	2	3	2
Carya spp.	1	1	1	3
Castanea dentata	1	1	3	3
Catalpa spp.	1	1	1	2
Celtis spp.	1	1	1	2
Fagus grandifolia	3	1	2	3
Fraxinus spp.	1	1	1	2
Gleditsia triacanthos	1	1	1	2
Gymnocladus dioicus	1	1	1	2
Ilex opaca	3	2	2	3
Juglans spp.	2	1	1	2
Liquidambar styraciflua	3	2	2	1
Liriodendron tulipifera	3	2	3	3
Magnolia spp.	3	3	2	3
Nyssa spp.	3	2	3	1
Platanus occidentalis	3	1	1	3
Populus spp.	3	1	3	3
Prunus serotina	3	1	3	3
Quercus spp.	1	1	3	2
Robinia pseudoacacia	1	1	1	2
Salix nigra	3	1	2	2
Sassafras albidum	1	1	3	2
Tilia spp.	3	1	3	2
Ulmus spp.	1	1	3	3

[a] Pore arrangement: 1, ring porous; 2, semi-ring porous; 3, diffuse porous.
[b] Perforation type: 1, simple perforation; 2, scalariform perforation; 3, exhibits both types.
[c] Ligulate tip shape: 1, mucronate (terminates abruptly); 2, attenuate (tapering gradually); 3, exhibits characteristics of both.
[d] Ligulate tip overlap: 1, major; 2, minor; 3, exhibits characteristics of both.

highly inclined position to the transverse position as the scalariform perforation develops into the simple perforation. This inclination of the end wall could also be related to ligulate tip shape and to the overlap of the ligulate tip between successive vessel elements. The relationship of vessel perforation type and ligulate tip overlap had a probability of 0.048. Genera with simple perforations had a greater tendency to exhibit ligulate tips with minor overlap, and genera with scalariform perforations exhibited a greater tendency towards ligulate tips with major overlap. Again, approximately 50% of the genera examined exhibited characteristics of both major and minor overlap of the ligulate tip.

The relationship between pore pattern and ligulate tip overlap had a probability

TABLE 2. *Vessel characteristic distributions evaluated by chi-square.*

Characteristics compared	Chi-square probability
Pore arrangement—perforation type	0.109
Pore arrangement—ligulate tip	0.065
Pore arrangement—ligulate tip shape	0.042
Perforation type—ligulate tip overlap	0.048
Perforation type—ligulate tip shape	0.017

of 0.065. Ring porous genera and semi-ring porous genera exhibited ligulate tips with minor overlap between successive vessel elements. Diffuse porous genera had both major and minor overlap of the ligulate tip between successive vessel elements.

CONCLUSION

The ligulate tip, a structure with various forms on hardwood vessel elements, is a morphological artifact resulting from the evolutionary specialization of ring porous genera. Attenuate tips are more primitive than mucronate tips. This conclusion is based on the statistical comparisons of vessel morphology and arrangement coupled with the premise that ring porosity is an indication of evolutionary advancement in angiosperms (Esau 1977).

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