WOOD AND LEAF ANATOMY IN SESSEA CORYMBIFLORA FROM AN ECOLOGICAL PERSPECTIVE

by

Helga Lindorf

Centro de Botánica Tropical, Facultad de Ciencias, Universidad Central de Venezuela, Apartado 20513, Caracas, Venezuela

SUMMARY

The wood and leaf structure of *Sessea corymbiflora*, a new species for the Venezuelan solanaceous flora, are described and compared from an ecological perspective. In accordance with the humid environment where the plant grows and its position in an intermediate layer of the forest, a predominantly mesomorphic wood and a mesomorphic leaf structure with intermediate features between sun and shade types (medium leaf type) are developed. Xeromorphic traits are also found, however: vasicentric tracheids and vessel grouping in the wood; thick cuticle and cutinized outer epidermal wall in the leaf. The existence of these adaptations is discussed in relation to microclimate and the effect of seasonal dry periods. The possible influence of altitude is also considered.

**Key words:** *Sessea*, Solanaceae, ecological wood anatomy, ecological leaf anatomy.

INTRODUCTION

*Sessea corymbiflora* Goudot ex Taylor & Phillips is an evergreen shrub or tree to 16 m tall with stems reaching 20–50 cm diameter, and with coriaceous or firmly membranous leaves of up to 20 cm in length, glabrous or occasionally bearing reduced trichomes. It is found in dense forests at high altitudes (2200–2800 m in Venezuela–Colombia and up to 3500 m in Ecuador) on rocky soils in subparamo areas. In Venezuela it is restricted to the western Andean region where it was only recently discovered (Benítez & D’Arcy 1993). *Sessea* is also a new genus for the solanaceous flora of Venezuela as it had before only been reported in Colombia, Ecuador, Peru and Brazil. It belongs to the subfamily Cestroideae, showing a great deal of similarity in its vegetative morphology and flowers with *Cestrum*, although the fruits and seeds are clearly distinguishable.

There is no information about the wood and leaf anatomy in *S. corymbiflora*. Regarding the other species of the genus, the only known references are the observation of Solereder (1908), summarized again by Metcalfe and Chalk (1950), about candelabra hairs in *S. vestita*, and the papers of Coleman (1966) and Pinho et al. (1986) concerning, respectively, the leaf and wood anatomy of *S. brasiliensis*. Carlquist (1992) did not include *Sessea* in his work on the wood anatomy of the Solanaceae. In this
study, he observed a wide range of secondary xylem features in the family concluding that this range represents more numerous instances of ecological patterning of wood than character state distributions, which relate primarily to taxonomic grouping.

As is well known, climatic factors such as temperature and water availability, as well as geographical variables including latitude and altitude, correlate with dimensions and density of the perforated tracheary elements and with other characteristics of the xylem tissues (Baas 1973, 1976, 1982, 1986). In general, secondary xylem from species in xeric floras commonly have numerous vessels with short and narrow elements, which leads to greater conductive safety. The xylem of species from mesic floras, by contrast, is connected with a higher efficiency but lower safety, given the predominance of fewer but wide vessels in an equivalent area. As ecological indicators in relation to the wood, Carlquist (1977) conceived two indices: Vulnerability (mean vessel diameter divided by mean vessel frequency) and Mesomorphy (vulnerability multiplied by mean vessel element length). High values of V and M (more than 1 and 800, respectively) indicate adaptation to mesic, whereas low figures (less than 1 and 50, respectively) to xeric conditions (Carlquist 1977, 1992). Some authors have argued lack of predictive or functional significance for these concepts, based on the fact that in some cases the values obtained show a tremendous range despite the uniformity of the habitat (Van den Oever et al. 1981). Carlquist (1988) is of the opinion that these deviations may also have an important value, predicting the action of special strategies or of mitigating effects due to other plant features. The majority of studies on the adaptive nature of the conducting system in dicotyledons has been carried out in areas of marked water stress. Yet the principle of conduction in mesic areas is still far from being fully understood.

The adaptability of the leaves to the environment has been recognized for longer than that of wood (see Napp-Zinn 1984). Roth (1984), in her study on a humid forest in Venezuelan Guayana, stressed the influence of the microclimate on leaf structure and noted that in the upper strata of vegetation (trees over 30 m tall) xeromorphic features predominate, while in the lower strata (small trees and shrubs under 10 m) hygromorphic characteristics prevail; she also related the sun leaf anatomy with the upper strata and the shade leaf type with the understory. In the intermediate strata (trees between 10 and 29 m tall) she reported a predominance of the mesomorphic structure and medium leaf type (intermediate features between sun type and shade type). Pyykkö (1979), in her study of 22 species in a Venezuelan rain forest in the Guayana region, concluded that the leaf anatomy in this environment is homogeneous and moderately mesomorphic. Lindorf (1992, 1993), analysing 28 species from a rain forest in the Amazon region of Venezuela, identified a certain general tendency to the mesomorphic type but also reported various xeromorphic and sun leaf features not only in trees and climbers but among shrubs too, which she attributed to microclimatic effects as indicated by Roth, and to the possibility of seasonal dry spells.

Carlquist (1975a, 1977, 1980), Baas (1982), and Rury & Dickison (1984) all recognized the need to integrate the knowledge on ecological wood anatomy with information about other organs of the plant, especially leaves and roots. Some studies have been carried out along these lines (Michener 1981; Rury 1981; Rury & Dickison 1984;
Lindorf 1994). The present work, dealing with the wood and leaf anatomy of *Sessea corymbiflora*, was approached from this perspective. It is hoped that the anatomical data will also contribute to a better characterization of this species.

**MATERIALS AND METHODS**

Material was collected from a tree 8–10 m tall with a stem diameter of 30 cm, growing at 2500 m above sea level (Benítez et al. 4839), and from another one 5 m tall with a stem diameter of 15 cm, at 2600 m (Benítez & Rojas 5373). In both cases samples of wood and leaf were taken and preserved in alcohol. The collection area corresponds to evergreen cloud forests in the Venezuelan Andean region located at approximately 8° N latitude, with a mean temperature of 10–16 °C, a mean yearly rainfall close to 2000 mm (including a dry period between November and March) and a high relative humidity in the order of 80–100%. Transverse, tangential, and radial sections of the wood were cut with a sliding microtome. Transverse and paradermal sections of the leaf were made by hand and with the sliding microtome using no embedding procedures but holding the leaf pieces between sheets of polystyrene. Macerated wood tissue was prepared according to Franklin (1946) while epidermal leaf peels were made with the Jeffrey maceration method (Johansen 1940), but allowing the mixture to act for only 20 minutes. The resulting preparations were stained with toluidine blue or safranin and mounted in Euparal. Terminology and the method for determining quantitative features in the wood conform to recommendations from the IAWA Committee (1989). For vessel multiples each pore was counted as a unit; vessel element length was measured including tails. The eco-anatomical characterization of the leaf was carried out according to Roth (1984). For each character, means and maximum and minimum values were determined. Vessel frequency and stomatal density were obtained from counts in ten areas of 1 mm² each. For the remaining features, values were based on 25 measurements.

**RESULTS AND DISCUSSION**

*Wood description* (Fig. 1–11)

Growth rings absent. Wood diffuse-porous. Vessels 22 (15–28)/mm², usually in radial multiples of 2–6, sometimes clustered, 8–10% solitary with more or less circular outline, tangential diameter 94 (74–123) μm, some narrower. Vessel elements 630 (492–775) μm long, with short or long tails. Perforation plates simple, sometimes 2 per end wall. Intervessel pits non-vestured, alternate, bordered, circular, 6 μm. Vasicentric tracheids present. Vessel-ray and vessel-axial parenchyma pits simple, horizontal and elongated. Fibres 1150 (924–1500) μm long, thin-walled, with simple pits, septate or not. Axial parenchyma scanty paratracheal, in strands of 2–4 cells; apotracheal diffuse parenchyma occasionally present. Rays 3 (2–4)/mm, uniseriate 361 (180–864) μm tall, but mainly multiseriate, 2–6 cells or 63 (37–86) μm wide, 552 (240–852) μm tall, Kribs heterogeneous type II with 1–6 rows of upright/square marginal cells; marginal cells sometimes present in only one of the ends or completely absent;
sheath cells present but not totally encircling the ray, occasionally very tall. Starch grains common in septate and non-septate fibres and in the ray cells. Crystals absent.

Pinho et al. (1986), in their study on the wood anatomy of several arboreal Solanaceae in Brazil, reported the absence of axial parenchyma in Sessea brasiliensis. However, in the present study the existence of this tissue has been demonstrated, albeit scarce (Fig. 3, 4). In S. corymbiflora, moreover, up to two perforation plates may occur on
Fig. 6–11. Wood anatomy of *Sessea corymbiflora*. – 6: Tangential section showing predominance of multiserate rays. – 7: Radial section. – 8: Vasicentric tracheids. – 9: Simple pitting in ray cells. – 10: Starch grains in a fibre. – 11: Portion of a septate fibre showing septum (arrow). — Scale bars: 6, 7 = 200 µm; 8–11 = 50 µm.

one end wall (Fig. 2), a feature not previously reported in *Sessea brasiliensis*, although mentioned with regard to other Solanaceae (Murthy et al. 1980; Carlquist 1992). Another feature not noticed in *Sessea brasiliensis* is the presence of septate fibres and vasicentric tracheids, which, by contrast, constitute a characteristic trait of *S. corymbiflora* (Fig. 8, 10, 11). The correlation observed in *S. corymbiflora* between presence of septate fibres containing starch, and absence or scarcity of axial paren-
Fig. 12–18. Leaf anatomy of *Sessea corymbiflora*. – 12: Cross section showing mesomorphic structure. – 13: Upper epidermis. – 14: Midvein in cross section. – 15: Lower epidermis with stomata. – 16 & 17: Glandular hairs. – 18: Detail of upper epidermis showing thick cuticle and anticlinal ‘pegs’. — Scale bars: 12, 13, 15–18 = 50 μm; 14 = 200 μm.
chyma has also been reported in other species (Harrar 1946; Carlquist 1975a, b; Wolkinger 1970). For this type of fibre it has been postulated that they could serve in storing and transport of photosynthates, acting as a substitute for axial parenchyma though they would not be so efficient owing to mechanical resistance. Braun (1984), explaining his hypothesis concerning a second principle of water ascent based on an osmotic water shifting, suggested that in tropical trees the masses of starch observed in wood are not reserves but simply deposits of an osmotically inactive product of surplus carbohydrates.

Leaf description (Fig. 12–18).

Dorsiventral, hypostomatic, 213 (111–256) μm thick. Upper epidermis unilayered, with relatively thick (6 μm) cuticle forming pegs that penetrate the anticlinal walls; outer wall thin, sometimes partly cutinized; epidermal cells with straight or slightly sinuous anticlinal walls and lightly striated cuticle. Palisade parenchyma 1- or 2-layered, 109 (92–128) μm thick. Upper palisade cells 57 (48–64) μm long, but much shorter in the inner layer; transitional layer, partly with funnel-shaped collecting cells, located below the palisade. Palisade parenchyma not extending over the midvein or secondary veins. Spongy parenchyma loose, 5- or 6-layered with some of the layers parallel to the surface, 88 (72–100) μm thick. Palisade/spongy ratio 1.2:1. Lower epidermis unilayered with cuticle and outer wall of approximately the same thickness as those of the upper epidermis; epidermal cells polygonal, with slightly sinuous anticlinal walls. Stomata anomocytic, level with leaf surface, with cutinized ledges, 162 (148–180)/mm², guard cells 40 (31–50) μm long. Scanty glandular hairs adpressed on both surfaces of the leaf, with a short stalk and a bi-cellular head. Secondary veins with non-transcurrent collateral bundles, separated from each other by a distance of 221 (160–280) μm, and surrounded by a parenchymatous sheath of lignified cells with large pits; sclerenchyma occasionally separating phloem and xylem. Secondary and tertiary veins with bundles separated from the epidermis by collenchyma layers; in veins of higher order the vascular bundles are embedded in the spongy parenchyma. Midvein with the vascular tissues bicolateral, arranged in an arc surrounded by lignified cells (3 or 4 layers), especially towards the lower surface. Parenchyma occurring external to this sclerenchyma sheath, followed by collenchyma which extends to either epidermis. Midrib protruding both abaxially and adaxially where it appears like a ridge, taking the aspect of a dome in cross section (Fig. 14).

The leaf anatomy of *S. corymbiflora* is similar in many features to *S. brasiliensis*, though differing in the absence of candelabra hairs, but having glandular hairs (Fig. 16, 17). In this character it differs also from *S. vestita*, the only other *Sessea* species where observations on leaf anatomy have been made (Solereder 1908; Metcalfe & Chalk 1950). Unfortunately, this comment on its type of indument is the only information given. Furthermore, what is also characteristic of *S. corymbiflora* and not reported for *S. brasiliensis* are the cuticular pegs (especially in the upper epidermis) which penetrate the anticlinal walls almost to half its length (Fig. 18).
Table 1. Wood anatomical features of *Sessea corymbiflora* and comparison with data available for other species.

<table>
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<th>Sessea corymbiflora</th>
<th>Sessea brasiliensis (1)</th>
<th>Solanaceae from tropical rain forests (2)</th>
<th>Species from La Mucay cloud forest (3)</th>
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</table>
| Tangential vessel diameter (µm)      | 94  
(74–123)            | 60–90                   | 108  
(75–161)                               | 124  
(62–205)                               |
| Vessels per sq.mm (4)                | 22  
(15–28)             | 30–50                   | 13  
(5–18)                                   | 13  
(3–64)                                   |
| Vessel element length (µm) (5)       | 630  
(492–775)           | 300–640                 | 425  
(321–564)                             | 697  
(280–1516)                             |
| Number of vessels per group          | 2  
(1–6)               | –                       | 2  
(1–2)                                   | –                                         |
| Intervessel pit size (µm)            | 6  
(6–12)               | –                       | 10  
(6–12)                                 | –                                         |
| Fibre length (µm)                    | 1150  
(924–1500)          | 1100                    | 783  
(123–1234)                             | –                                         |
| Vulnerability                        | 4.2                   | 1.8–2                   | 8.3  
(9.5)                                  |                                          |
| Mesomorphy                           | 2677                  | 540–1280                | 4416                             | 8252                                   |
| Multiseriate ray height (µm)         | 552  
(240–852)           | –                       | 452  
(170–1526)                             | –                                         |
| Multiseriate ray width (µm)          | 63  
(37–86)             | –                       | –   
(–)                                     | –                                         |
| Uniseriate ray height (µm)           | 361  
(180–864)           | –                       | 172  
(68–434)                             | –                                         |
| Number of rays per mm                | 3  
(2–4)               | –                       | –   
(–)                                     | –                                         |

(1) From Pinho et al. (1986), no means reported. – (2) From Carlquist (1992). – (3) From Pérez Mogollón (1989). – (4) For vessel multiples, each pore was counted as a unit. – (5) Measured including tails.

**Eco-anatomical aspects**

From Table 1 we can observe that *S. corymbiflora* possesses both V and M values that can be classified as mesomorphic according to the criteria established by Carlquist (1977, 1992). Comparing the data of *S. corymbiflora* with the information presented by Carlquist (1992) for 11 solanaceous trees and shrubs from tropical rain forests, and
with the results of Pérez Mogollón (1989) for 40 species of La Mucuy cloud forest from different families, we observe, however, that in *S. corymbiflora* the V and M indices are lower, and the vessels narrower and more numerous, indicating then a slightly higher safety while still evidencing conductive efficiency. Vessel element length values are more or less similar except in the species reported by Carlquist (1992) where they are shorter.

In the table quantitative characteristics are included of *S. brasiliensis*, which is found in Brazil at latitudes between 23–24° S and on elevations ranging from 700 to 1000 m above sea level (Pinho et al. 1986). The figures show that in this species vessels tend to be more numerous, with smaller diameter and shorter elements than in *S. corymbiflora*. Without forgetting that this information was based on only one specimen and that the latitudinal range is not very extensive, these data seem to concur with the miniaturization of secondary xylem elements and the increase in vessel frequency associated with increasing latitude, observed by various authors (Van der Graaff & Baas 1974; Van den Oever et al. 1981). Nevertheless, it would be important to have climatological data from the locality of provenance of the *S. brasiliensis* sample in order to discard the effect of other factors. Vessel element length is higher in the two *Sessea* species than the values of 300–400 μm reported by Metcalfe and Chalk (1950) for the family. Likewise, it surpasses the means of 340 μm and 400 μm calculated from Carlquist (1992) for the total of Solanaceae investigated and for those from rain forest, respectively. As this author pointed out, only one collection of one species in the family, *Duboisia myoporoides*, a temperate tree, rises to the level of 649 μm reported by Metcalfe and Chalk as the mean for the dicotyledons as a whole. Long vessel elements are thus infrequent in Solanaceae and its occurrence in *Sessea*, where it appears to be a generic character, maybe useful for taxonomic purposes; at the same time it can be considered a mesomorphic feature. The high value for vessel element length is ultimately reflected in the mesomorphy index of this species.

In *S. corymbiflora* only 10% of the vessels can be classified as solitary, while the rest are multiples with a mean number of 2 vessels per group. Tracheids are adjacent to some of the vessels in variable numbers. This combination of vasicentric tracheids and multiple vessels that occurs in *S. corymbiflora* (Fig. 1, 8) is worth mentioning because both features have been associated with conductive safety (Carlquist 1966, 1984, 1985, 1987).

Leaf anatomy of *S. corymbiflora* appears to be consistent with the humid environment and the position of the tree in an intermediate stratum of the forest. A predominance of mesomorphic features associated with a medium leaf type (intermediate features between sun and shade types) are therefore expected. The most obvious mesomorphic traits present in this species are: medium thickness of the blade, absence of water storing tissues, medium consistency of the mesophyll, stomata level with the epidermis, absence of an extensive hair cover. The size of its epidermal cells, the frequency of the vascular bundles (determined by the distance between them), and the degree of development of the bundle sheaths are also consistent with a mesomorphic type of structure. The medium leaf type can be deduced from the size of the outer pali-
sade cells which are not as long as in sun types nor so short as in the shade leaves. Roth (1984), for instance, reported lengths of 80–135 μm for palisade cells in some trees from the upper stratum of a humid forest in Venezuelan Guayana. Another indication of the medium leaf type is that the thickness of the palisade only just surpasses that of the spongy parenchyma. The relatively low stomatal density values and the great size of the guard cells in this species, nevertheless, correspond more closely to hygromorphic characteristics. A density of 100–200 stomata per mm² is reported by Roth (1984) for hygromorphic shade leaves. Regarding the size, the values for the guard cells observed in S. corymbiflora are similar to those of plants of the lower stratum of cloud forests (Lindorf 1980a, b; Roth 1990). Although the leaf of S. corymbiflora is predominantly mesomorphic, with some hygromorphic traits, it also shows one important xeromorphic characteristic in its thick cuticle and the cutinization of the outer walls (Fig. 12, 18).

The leaf epidermis with thick cuticle and cutinized outer walls, and the relatively numerous and narrow vessels, predominantly in groups, together with the presence of vasicentric tracheids in the wood, suggest an adaptation of S. corymbiflora to survive conditions of water stress. According to Longman and Jenik (1974) there is a tendency to exaggerate the frequency of rain, saturation of air with water vapour, swampiness of soil and absence of water deficits in tropical regions. Coutinho (1962) reported short dry spells in rain forests in Brazil. Huber (1986) reported a drop in rainfall and relative humidity in the cloud forest of Rancho Grande in Venezuela. In the localities where S. corymbiflora is found there is usually a period of low rainfall between November and March, to which the desiccating effect of winds is added. In La Mucuy forest, with similar environmental characteristics, fluctuations in rainfall have been determined, with 1.2 to 2 dry months per year (Lamprech 1954). Though the findings of Pérez Mogollón (1989) for trees in this forest showed woods with a predominance of moderately numerous vessels, medium-sized in diameter, with medium-sized elements, he also indicated a certain proportion of narrow (29%) and of numerous (32%) vessels, which could both be responses to the occurrence of dry periods. The percentage of short vessel elements is low (13%), however, suggesting that this feature might not respond in the same way as the other two mentioned.

A possible effect of altitude in the structure of S. corymbiflora should not be discarded. This factor may have a bearing in the increase in vessel frequency and the narrowness of the elements; likewise, the thick cuticle and the cutinization of the outer wall in its leaf epidermis could also be related not only with dry climatic periods, but also with the strong irradiation prevailing at high altitudes.

Studying correlations between the wood and leaf of various species, Rury and Dickison (1984) identified cases in which the xylem and the leaf have evolved together as a unit showing both adaptations correlated to environmental extremes, whereas in others, only the leaf shows adaptations, leaving the wood at a low level of specialization. According to the results here presented, Sessea corymbiflora seems to be an example of the first strategy, although the information available does not confirm that it is really submitted to extreme conditions.
ACKNOWLEDGEMENTS

This study was supported by funds from the Consejo de Desarrollo Científico y Humanístico de la Universidad Central de Venezuela (03.SP.001.95). I am very grateful to Profs. William G. D’Arcy and Carmen Benítez de Rojas, proposers of this research, who kindly collected the samples and provided papers not otherwise available in Venezuelan libraries. Thanks are also due to Ms. Alexandría Jiménez for her technical assistance.

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