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WOOD ANATOMY OF NOLANACEAE

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ABSTRACT

Wood of seven collections of six species of *Nolana,* a genus (18 spp.) of the central western coast of South America was studied for quantitative and qualitative features. The wood is ring porous, with moderately wide vessels bearing simple perforation plates and alternate pits with some grooves interconnecting slitlike pit apertures. Imperforate tracheary elements are fiber-tracheids with vestigial borders on pits or libriform fibers; vasicentric tracheids (reported for Nolanaceae for the first time) are present in varying numbers. Axial parenchyma is vasicentric scanty (sometimes absent), sometimes with tangential bands that may be terminal in part. Rays are both multiseriate and uniseriate; ray cells are mostly erect. Crystal sand occurs in some ray cells and some axial parenchyma. The sum of features mark Nolanaceae as very close to Solanaceae. Wood of *Nolana* varies in xeromorphy; lower degrees of xeromorphy may be explained by succulence related to maritime habitat or to ephemeral nature of stems. The erect nature of ray cells and a decrease in vessel element length are indicators of paedomorphosis and thereby herbaceousness of Nolanaceae.

Key words: Convolvulaceae, crystal sand, Nolanaceae, Solanaceae, vasicentric tracheids, wood anatomy.

INTRODUCTION

In recent years, Nolanaceae have been considered sufficiently close to Solanaceae so that some authors include them in the latter as a tribe, Nolaneae (Dahlgren 1980; Takhtajan 1980; Thorne 1983). However, an equal number of authorities could be cited who maintain Nolanaceae as a family (Cronquist 1981; Endress 1981; Hunziker 1979; Mesa 1981). Nolaneae were originally considered as a tribe of Convolvulaceae by Bentham and Hooker (1873–1876). The family is noteworthy for subdivision of carpel primordia (Endress 1981) to form nutlets, which range from three to 27 in number (Mesa 1981). The presence of intraxylary phloem (phloem between pith and primary xylem) in Nolanaceae (Mirande 1922) has been considered a link between Nolanaceae and Solanaceae, as has the occurrence in wood of crystal sand (Metcalfe and Chalk 1950), a distinctive feature in woods. The present investigation examines the degree of closeness between Nolanaceae and Solanaceae. There has been no previous monograph of wood in Nolanaceae. The present paper is part of a survey of wood anatomy of tubiflorous dicotyledon families in an attempt to aid definition of natural groupings of families and find their interrelationships.

Nolanaceae are considered to have a single genus of 18 species, *Nolana,* by Mesa (1981). Mesa considers as sections *Alona* (style terminal, ovary not deeply subdivided, nutlets 3–6, united along their length to the columella) and *Nolana* (style basal, nutlets 3–27, adherent to the disc by their bases). The former genus *Bargemontia* is considered a subsection of section *Nolana*; *Dolia* becomes a synonym of *Nolana.*

Nolanaceae are distributed along the western coast of South America from Chiloe I., Chile, northwards to central Peru; one species occurs on the Galapagos Islands (Mesa 1981). Mesa recognizes 18 species of *Nolana.* One cannot expect at the species level a correlation between wood anatomy and ecology in all species. For example, *N. crassulifolia* Poepp. subsp. *crassulifolia* ranges from inland to the immediate seacost. At the latter sites, plants of this taxon are more strongly succulent. Nolanaceae often occur in dry or saline sites. Although one should look at wood anatomy of the family with respect to ecology, modifying factors (e.g., ephemeral foliage) must be considered and close correlations to habitat severity need not necessarily be expected.

Wood anatomy of Nolanaceae is of interest with respect to the habits within the family. Although Nolanaceae range from annuals to shrubs, the latter seem not strongly woody, and the family as a whole may be termed herbs or somewhat woody herbs.

MATERIALS AND METHODS

All wood samples represent stems from dried samples. One of these was collected in the field (*N. crassulifolia* subsp. *crassulifolia, Carlquist 7325,* north of San Antonio, Chile). Wood of the remaining collections was obtained from specimens at the U.S. National Herbarium. These collections and the localities from which they came are: *N. adansoni* (Feuillee ex Roem. & Schules) Johnst., *Mexia 7773,* south of Mollendo, Peru; *N. crassulifolia* subsp. *crassulifolia, Johnston 5014,* near Copiapo, Chile; *N. humifusa* (Gouan) Johnst., *Ferreyra 2560,* between Camarc and Arequipa, Peru; *N. peruviana* (Gaud.) Johnst. subsp. *divaricata* (Lindl.) Mesa, *Werdermann 461,* 30 km north of Caldera, Chile; *N. rostrata* (Lindl.) Miers var. *carnosa* (Lindl.) Mesa, *Johnston 5047,* dunes north of Caldera, Chile; *N. sedifolia* Poeppig subsp. *confinis* (Johnst.) Mesa, *Hutchinson 1846,* 50 km north of Tacna, Peru. Determinations are according to Mesa, who has annotated these specimens. One could consider that seven collections of six species respresent an insufficient survey in a genus that contains 18 species. However, the majority of taxa not included are plants of smaller stature. In these, study of wood anatomy is inappropriate not merely because of the small size, but because data yield of a short span of secondary xylem is minimal and dubiously comparable to that from older stems.

Wood samples were boiled and stored in aqueous 50% ethyl alcohol. Portions were sectioned on a sliding microtome; sections were stained with safranin and counterstained with fast green. Stems of *N. crassulifolia* subsp. *crassulifolia, Carlquist 7325,* were too pliable to section on a sliding microtome; therefore, they were softened in ethylene diamine and sectioned in paraffin (Carlquist 1982). Macerations of all taxa were prepared with Jeffrey's Fluid and stained with safranin. For quantitative features, means are based on 25 measurements except in the case of vessel wall thickness, imperforate tracheid element diameter, and imperforate tracheid element wall thickness; for these three features, means are based upon several measurements. Figures for vessel diameter include the vessel wall. Collection of the wood sample of *N. crassulifolia* subsp. *crassulifolia* was enabled by a grant from the National Science Foundation, DEB 81-09910. The present study was supported by N. S. F. grant BSR-8419469. I am grateful to Dr. Richard Eyde for access to the U.S. National Herbarium specimens of *Nolana.*

ANATOMICAL DESCRIPTIONS

NOLANA ADANSONI (*Mexia 7773*) (Fig. 1, 2).—Growth rings present; vessels and fiber-tracheids wider in earlywood (Fig. 1). Vessels variously clustered. Mean number of vessels per group, 2.52. Mean vessel diameter, 41 μm. Mean vessel wall thickness, 2.3 μm. Mean vessel element length, 255 μm. Mean number of vessels per mm^2, 255. Perforation plates all simple. Lateral wall pitting of vessels of alternate, circular to elliptical pits about 5 μm in diameter with narrowly elliptical pit apertures. Imperforate tracheary elements are all libriform fibers, borders not observed on pits. Mean diameter of libriform fibers, 25 μm. Mean wall thickness of libriform fibers, 2.2 μm. Mean libriform fiber length, 440 μm. Pits on libriform fibers slitlike, about 2 μm long. Axial parenchyma very scarce, vasicentric where present. Rays both multiseriate and uniseriate, the two types about equally abundant (Fig. 2). Ray cells predominantly erect; some square cells present, procumbent cells uncommon. Mean multiseriate ray height, 361 μm. Mean uniseriate ray height, 135 μm. Mean width of multiseriate rays at widest point, 2.32 cells. Ray cell walls relatively thin but lignified (Fig. 2). Wood nonstoried. Crystals absent in sample studied.

NOLANA CRASSULIFOLIA subsp. CRASSULIFOLIA (*Johnston 5014*) (Fig. 5, 6, 7).—Growth rings present, vessels wider in earlywood (Fig. 6). Vessels grouped, often in diagonally-oriented patches (Fig. 4). Mean number of vessels per group, 6.80. Mean vessel diameter, 29 μm. Mean vessel wall thickness, 2.2 μm. Mean vessel element length, 252 μm. Mean number of vessels per mm^2, 304. Perforation plates all simple. Lateral wall pits alternate, circular in outline, about 5 μm in diameter, with narrowly elliptical pits (Fig. 5). Imperforate tracheary elements are all libriform fibers, borders not observed on pits. Mean libriform fiber diameter, 11.5 μm. Mean libriform fiber wall thickness, 2.3 μm. Mean libriform fiber length, 399 μm. Pits on libriform fibers slitlike, about 2 μm long. Axial parenchyma rare, vasicentric, present in strands of two cells. Rays both multiseriate and uniseriate, the two types about equally abundant (Fig. 7). Ray cells predominantly erect, square cells rare and procumbent cells not observed. Mean height of multiseriate rays, 718 μm. Mean height of uniseriate rays, 224 μm. Mean width of multiseriate rays at widest point, 2.24 cells. Ray cell walls relatively thin but lignified. Wood nonstoried (Fig. 7). A few druses observed in ray cells. Crystal sand observed in a few ray cells and axial parenchyma cells. Resinlike deposits in some ray cells.

NOLANA CRASSULIFOLIA subsp. CRASSULIFOLIA (*Carlquist 7325*) (Fig. 4, 8, 9).—Growth rings present but somewhat indistinct, vessels wider in earlywood (Fig. 8). Vessels grouped variously (Fig. 8), few solitary. Mean number of vessels per group, 3.27. Mean vessel diameter, 58 μm. Mean vessel wall thickness, 4 μm. Mean vessel element length, 167 μm. Mean number of vessels per mm^2, 86. Perforation plates all simple (Fig. 9). Lateral wall pitting alternate, pits circular in outline, about 4.5 μm in diameter, grooves interconnecting pit apertures conspicuous (Fig. 4). Imperforate tracheary elements can be termed fiber-tracheids because minute borders (about 1 μm in diameter) were observed on pits. Mean fiber-tracheid diameter, 21 μm. Mean fiber-tracheid wall thickness, 4.0 μm. Mean fiber-tracheid length, 397 μm. Pits of fiber-tracheids with slitlike apertures about 3 μm long. An appreciable number of vasicentric tracheids observed in macerations. Axial parenchyma vasicentric scanty or in short tangential bands (Fig. 8,

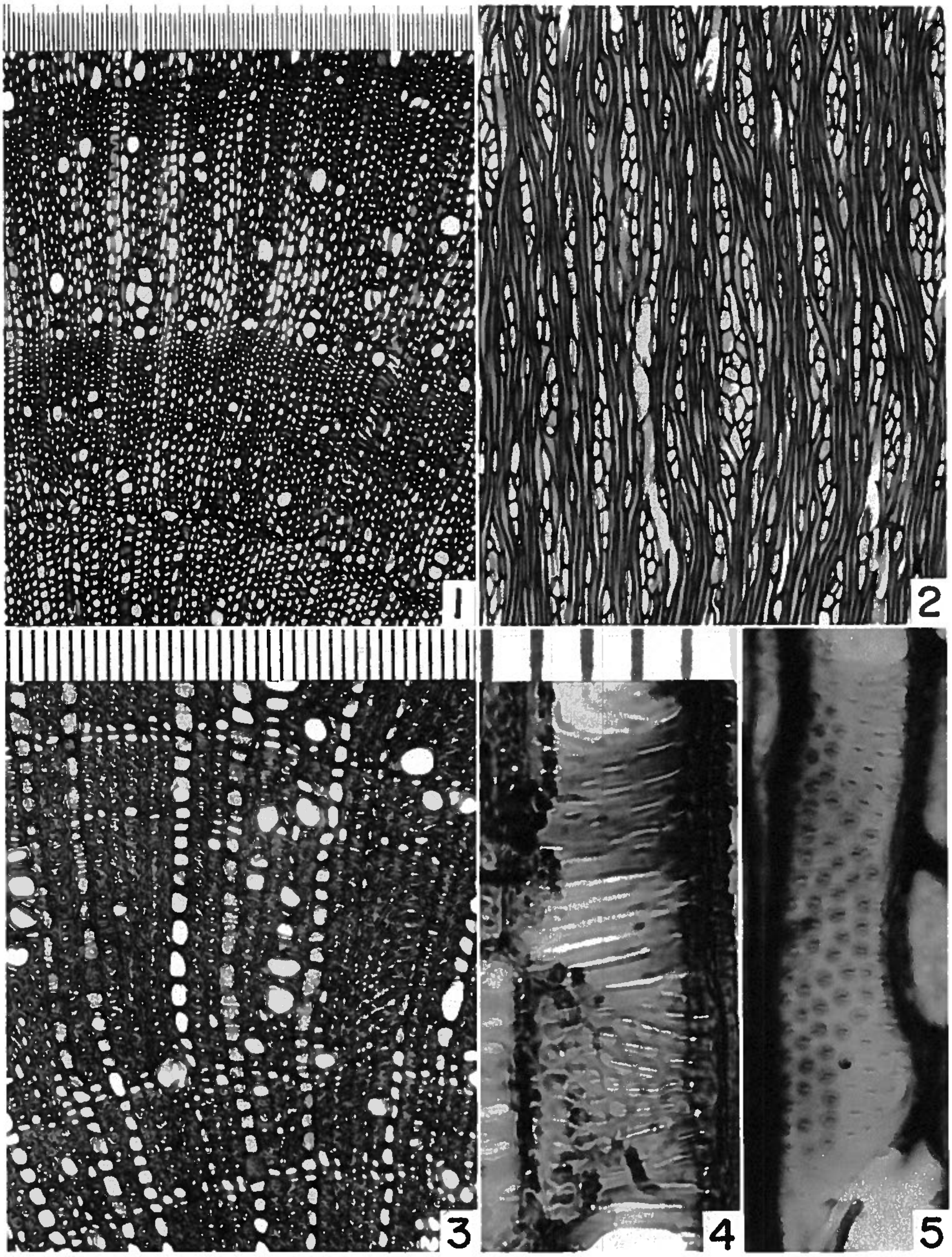

Fig. 1–5. Wood sections of *Nolana.*—1–2. *N. adansoni* (*Mexia 7773*).—1. Transection; growth rings evident in fiber diameter and vessel diameter.—2. Tangential section; uniseriate and multiseriate rays about equally abundant.—3. *N. peruviana* subsp. *divaricata* (*Werdermann 461*). Transection; several tangential bands of parenchyma of various length are present.—4–5. *N. crassulifolia* subsp. *crassulifolia*, vessel walls from tangential sections.—4. Vessel wall from *Carlquist 7325*; prominent grooves interconnect pit apertures.—5. Vessel wall from *Johnston 5014*; pits have narrow pit apertures, grooves not evident. (Magnification scale for Fig. 1–2 above Fig. 1 [finest divisions = 10 μm]; scale for Fig. 3 above Fig. 3 [divisions = 10 μm]; scale for Fig. 4–5 above Fig. 4 [divisions = 10 μm].)

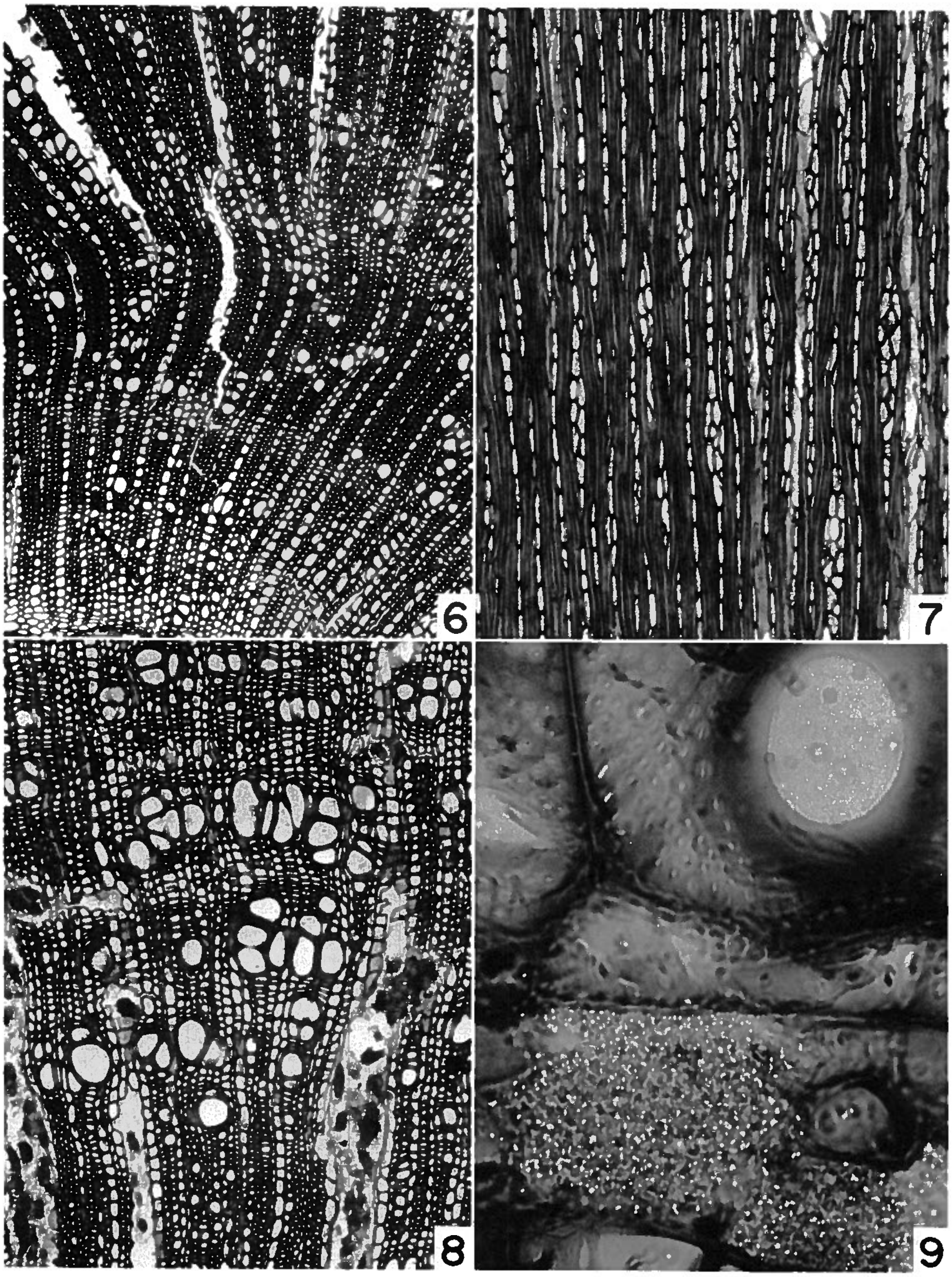

Fig. 6–9. Wood sections of *Nolana crassulifolia* subsp. *crassulifolia.*—6–7. Sections from *Johnston 5014.*—6. Transection; vessels grouped into diagonally-oriented aggregations.—7. Tangential section; ray cells are nearly all erect.—8–9. Sections from *Carlquist 7325.*—8. Transection; thin-walled ray cells have collapsed; masses of crystal sand appear as gray patches.—9. Portion of radial section, showing perforation plate (above) and crystal sand in ray cells (bottom third of photograph). (Fig. 6–8, magnification scale above Fig. 1; Fig. 9, scale above Fig. 4.)

left edge, just above center). Some terminal parenchyma bands also present. Parenchyma in strands of two or three cells. Rays both multiseriate and uniseriate, the two types about equally abundant. Most ray cells erect, some square and procumbent cells present. Mean height of multiseriate rays, 1210 μm. Mean height of uniseriate rays, 491 μm. Mean width of multiseriate rays not determined because of extensive breakdown of nonlignified walls in the centers of these rays; marginal cells of rays with thin but lignified walls (Fig. 8). Wood nonstoried. Crystal sand abundant in many ray cells, but also in some axial parenchyma cells (Fig. 8, 9). Adjacent groups of parenchyma cells tend to contain crystal sand.

NOLANA HUMIFUSA (*Ferreyra 2560*).—Growth rings clearly present, earlywood characterized by wider, thin-walled vessels and wider libriform fibers. Vessels variously grouped, few solitary; diagonally-oriented aggregations of vessels present. Mean number of vessels per group, 4.8. Mean vessel diameter, 34 μm. Mean vessel wall thickness, 1.7 μm (earlywood) to 2.8 μm (latewood). Mean vessel element length, 232 μm. Mean number of vessels per mm^2, 319. Perforation plates all simple. Lateral walls of vessels bearing circular pits about 2.8 μm in diameter, pit apertures narrowly elliptical. Imperforate tracheary elements are all libriform fibers, borders on pits not observed. Mean libriform fiber diameter, 14 μm (earlywood) to 28 μm (latewood). Mean libriform fiber wall thickness, 0.9 μm (earlywood) to 2.8 μm (latewood). Mean libriform fiber length, 419 μm. Vasicentric tracheids few. Axial parenchyma virtually absent, only two cells observed. Rays both biseriate and uniseriate, the latter more abundant. Ray cells predominantly erect, few square or procumbent cells seen. Mean multiseriate ray height, 199 μm. Mean uniseriate ray height, 114 μm. Wood nonstoried. Crystal sand observed in phloem parenchyma and parenchyma of primary xylem, but observed in very few ray cells in wood.

NOLANA PERUVIANA subsp. DIVARICATA (*Werdermann 461*) (Fig. 3).—Growth rings present, distinguished by wider vessels in earlywood; terminal parenchyma observed in latewood, although parenchyma bands elsewhere as well (Fig. 3). Vessels grouped, chiefly into diagonal aggregations. Mean number of vessels per group, 3.6 μm. Mean vessel diameter, 29 μm. Mean vessel wall thickness, 2.5 μm. Mean vessel element length, 222 μm. Mean number of vessels per mm^2, 209. Perforation plates all simple. Lateral wall pitting of vessels alternate, the pits circular in outline, about 3.2 μm in diameter; pit apertures narrowly elliptical, interconnected by grooves. Inconspicuos thickenings associated with the grooves. Imperforate tracheary elements can be termed fiber-tracheids; their pits have borders about 1 μm in diameter. Moderate numbers of vasicentric tracheids also present. Mean fiber-tracheid diameter, 14 μm. Mean fiber-tracheid wall thickness, 2.5 μm. Mean fiber-tracheid length, 391 μm. Pit apertures of fiber-tracheids slitlike, about 3 μm long. Axial parenchyma present as tangential bands (some of these terminal in growth rings), vasicentric parenchyma scarce. Rays both multiseriate and uniseriate, the latter more abundant. Multiseriate rays all biseriate. Erect and square cells relatively common, procumbent cells rare. Mean height of multiseriate rays, 374 μm. Mean height of uniseriate rays, 159 μm. Ray cell walls moderately thin but lignified. Wood nonstoried. Crystal sand observed in many ray cells.

NOLANA ROSTRATA var. CARNOSA (*Johnston 5047*).—Growth rings present, characterized by wider vessels in earlywood; some tangential parenchyma bands also observed in latewood. Vessels variously clustered. Mean number of vessels per group, 1.9. Mean vessel diameter, 26 μm. Mean vessel wall thickness, 2.5 μm. Mean vessel element length, 153 μm. Mean number of vessels per mm^2, 362. Perforation plates all simple. Lateral wall pitting of vessels alternate, pits circular in outline, about 2.4 μm in diameter, some grooves interconnecting pit apertures observed. Imperforate tracheary elements can be termed fiber-tracheids, since borders about 1 μm in diameter were observed on their pits. Vasicentric tracheids moderately abundant. Mean fiber-tracheid diameter, 11.5 μm. Mean fiber-tracheid wall thickness, 2.6 μm. Mean fiber-tracheid length, 338 μm. Apertures of fiber-tracheid pits slitlike, about 3 μm long. Some splits extending pit apertures seen; these probably are related to gelatinous nature of the fiber-tracheid walls. Axial parenchyma vasicentric scanty (not abundant) plus tangential bands most of which are terminal; parenchyma in strands of two cells. Rays uniseriate only. All ray cells erect. Mean uniseriate ray height, 191 μm. Ray cell walls relatively thin but lignified. Wood nonstoried. Crystal sand present in a few ray cells and in some axial parenchyma cells.

NOLANA SEDIFOLIA subsp. CONFINIS, (*Hutchinson 1846*).—Growth rings present, evident in wider vessel diameter in earlywood; thin-walled fibers present as a band in latewood. Vessels grouped variously. Mean number of vessels per group, 1.5. Mean vessel diameter, 54 μm. Mean vessel wall thickness, 2.2 μm. Mean vessel element length, 276 μm. Mean number of vessels per mm^2, 287. Perforation plates all simple. Lateral wall pitting of vessels alternate, pits circular in outline, about 3 μm in diameter, apertures narrowly elliptical. Imperforate tracheary elements may be termed libriform fibers because no borders could be clearly observed. Mean libriform fiber diameter, 14 μm. Mean libriform fiber wall thickness, 2.3 μm. Mean libriform fiber length, 422 μm. Pit apertures of libriform fiber pits slitlike, about 3 μm long. No axial parenchyma observed. Rays both multiseriate and uniseriate, both types about equally abundant. Mean multiseriate ray height, 662 μm. Mean uniseriate ray height, 1248 μm. Mean width of multiseriate rays at widest point, 2.2 cells. Ray cells moderately thin-walled but nonlignified. Wood nonstoried. No crystals observed.

CONCLUSIONS

Relationships of Nolanaceae

Nine critical features of Nolanaceae that may indicate relationship include (1) presence of simple perforation plates exclusively; (2) lateral wall pitting of vessels composed of alternate circular pits with narrowly elliptical apertures sometimes interconnected by grooves (rarely thickenings as well); (3) imperforate tracheary elements either fiber-tracheids with vestigial borders on pits or libriform fibers; (4) vasicentric tracheids present in various degrees of abundance; (5) vasicentric scanty axial parenchyma present, but tangential bands of axial parenchyma that are partly to wholly terminal present also, depending on species; (6) rays both multiseriate and uniseriate (rarely uniseriate only, and then only in juvenile wood); (7) ray cells predominantly erect, square and erect cells much less common to rare; (8) wood nonstoried; and (9) crystal sand (rarely druses) present in some ray and axial parenchyma cells. All of these features have been reported in Solanaceae (Metcalfe and Chalk 1950) except for terminal parenchyma. Most of the material presented by Metcalfe and Chalk on Nolanaceae is located under their account of Convolvulaceae, but they conclude that anatomy indicates relationship between Nolanaceae and Solanaceae. This is confirmed by such features as the occurrence of intraxylary phloem, present beginning at the hypocotyl in both families (Mirande 1922; Mesa 1981). Crystal sand, observed in most *Nolana* taxa here, is a particularly indicative feature. It occurs in woods of *Solanum* (Metcalfe and Chalk 1950), as well as those of *Nicotiana cordifolia* Phil., *Skottsberg 18* (original observation). In dicotyledons at large, crystal sand is present in parenchyma of woods in only a few families, such as Thymeleaceae. The occurrence of terminal bands of axial parenchyma does not appear to be an exceptional feature, for these bands are only partly terminal, and some of them, as in *N. peruviana* subsp. *divaricata* (Fig. 3) are short tangential bands, many of which are not terminal in growth rings; such tangential bands have been figured by Metcalfe and Chalk (1950, Fig. 227) for two species of Solanaceae, *Duboisia myoporoides* R. Br. and *Lycium acutifolium* E. Mey. Vasicentric tracheids, common in Nolanaceae, were not reported for Solanaceae by Metcalfe and Chalk but are now known for a number of Solanaceae, especially *Lycium* species (Carlquist 1985*a*). Taking into account reports of vasicentric tracheids in Cucurbitaceae and Polygonaceae (Carlquist 1985*b*), the reports of vasicentric tracheids in the present paper for various Nolanaceae brings the number of families containing those cells to 71, provided that Nolanaceae is recognized as a family.

Ecology

If one calculates the ratio termed "Mesomorphy" (vessel diameter times vessel element length divided by vessels per mm^2), the following figures for *Nolana* are obtained: *N. adansoni,* 14; *N. crassulifolia* subsp. *crassulifolia* (*Johnston 5014*), 24; *N. crassulifolia* subsp. *crassulifolia* (*Carlquist 7325*), 113; *N. humifusa,* 25; *N. peruviana* subsp. *divaricata,* 31; *N. rostrata* var. *carnosa,* 11; *N. sedifolia* subsp. *confinis,* 52. These values are certainly relatively low, but not as low as those of desert shrubs (e.g., Carlquist and Hoekman 1985). The case of *N. crassulifolia* subsp. *crassulifolia* is noteworthy; the Carlquist collection is from the immediate seacoast, where the plant is a halophytic stem and leaf succulent; the Johnston collection is from further inland and succulence is not so evident. Succulence does tend to be associated with wood more mesomorphic in character (e.g., Carlquist and Hoekman 1985). Mechanisms other than those of vessel dimensions and density may relate to the ability of Nolanaceae to live in dry habitats. Vessel grouping tends to be elevated in woods with fiber-tracheids and libriform fibers to the extent they occur in dry habitats (Carlquist 1984). Nolanaceae have moderately elevated figures for vessel grouping: the average for those studied is 3.5 vessels per group. Vasicentric tracheids may be an important factor in surviving drought (Carlquist 1985*a*). Nolanaceae have drought-deciduous leaves and also may sacrifice branches during dry seasons, so that the formulation of the wood is not of prime importance. In addition, some of the areas where Nolanaceae live receive fog condensation, a factor difficult to estimate in relation to others.

Ontogeny and Habit

The wood anatomy of Nolanaceae has several features that are indicative of paedomorphosis. Vessel element length apparently decreases with age: the relatively large stems of the Carlquist collection of *N. crassulifolia* subsp. *crassulifolia* have vessel elements much shorter than those of the Johnston collection, which had a much smaller stem. Ray histology can change with age, but in none of the Nolanaceae studied are procumbent cells common. Erect cells are common in rays of herbs and herblike plants (Carlquist 1962). All Nolanaceae can be considered essentially herbaceous with degrees of woodiness ranging from very little (annuals) to moderate (the largest woody cylinder in the family probably does not exceed a centimeter). In typically woody plants, rays with an abundance of procumbent cells would be expected.

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