



Stem and root anatomical correlations with life form diversity, ecology, and systematics in *Moringa* (Moringaceae)

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Four life forms (habits) are identified in the 13 species of *Moringa* (bottle trees, sarcorhizal trees, slender trees, and tuberous shrubs) which are examined for wood anatomical correlations with habit, ecology, and systematics. Wood anatomy is similar within habit classes except for the sarcorhizal trees. The four bottle tree species and *M. arborea* (one of the sarcorhizal trees) are characterized by bands of confluent paratracheal parenchyma alternating with bands of libriform fibres, some of which may be parenchyma-like. The other sarcorhizal tree, *M. ruspoliana*, is characterized by alternating bands of parenchyma-like and long, slender libriform fibres. Root secondary xylem of all these species is characterized by bands of parenchyma and fibres. Slender trees do not show bands of fibres of different shapes and have fibrous roots with less parenchyma than the other species. Tuberous shrubs have stems mostly composed of long, slender fibres and large underground tubers mostly composed of parenchyma. Quantitative trends between ecologically different localities include wider vessel elements and higher conductive area in moister localities. Wood anatomy provides characters that are of potential phylogenetic utility at a variety of levels of relationship. Based on wood anatomy and geography, the most likely sister taxon to *Moringa* is *Cylicomorpha* (Caricaceae).

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ADDITIONAL KEYWORDS: Capparales – Caricaceae – dry tropics – glucosinolate families – mustard-oil plants – systematic wood anatomy.

INTRODUCTION

Moringa, the sole genus of Moringaceae, is for its size one of the most phenotypically varied groups of angiosperms. With just 13 species throughout the dry tropics of the Old World, *Moringa* spans a vast range of life form (habit), from massive 'bottle trees' in Madagascar and Africa, to slender trees in Arabia and India, to shrublets with ephemeral shoots and underground tubers in northeast Africa (habit of each species is illustrated in Figures 1, 5, 9, 13, 17, 21, 25, 29, 33, 37, 41, 45, and 49). Diversity of form is a characteristic shared by many plant groups in dry tropical habitats, which are thought to support the

world's highest diversity of plant life forms (Medina, 1995). However, most research has been directed at wet forests and timber trees, and little is known about the anatomical correlates of the great diversity seen at the morphological level in dry tropical plants.

The present study examines variation in stem and root anatomy associated with habit in all 13 species of *Moringa* to test the assumption that habitual differences are associated with anatomical differences. An attempt is made to differentiate between anatomical differences associated with habit and intraspecific variation resulting from plastic responses to differing environmental conditions both between populations and within individuals across seasons. Descriptions of the anatomy of individual *Moringa* species are available in Olson (in press).

A sister-family relationship of the Moringaceae with

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the Caricaceae is strongly supported by molecular phylogenetic studies (Gadek *et al.*, 1992; Chase *et al.*, 1993; Rodman *et al.*, 1996). This view contrasts with previous systematizations (e.g. Dahlgren, 1975; Cronquist, 1981), none of which explicitly recognized a close relationship between the Moringaceae and Caricaceae. Thus it is of interest to examine the anatomy of the Moringaceae, as has been done for Caricaceae by Carlquist (1998), in light of this recent phylogenetic hypothesis. In addition to characters of potential interest at an interfamilial level, we evaluate our data for wood anatomical characters that provide potential phylogenetic information at an interspecific level.

Because of the remoteness of many *Moringa* localities, most previous studies of wood anatomy in *Moringa* (e.g. Metcalfe and Chalk, 1950; Ciuffi Cellai, 1971; Fahn, Werker & Baas, 1986) have focused on *M. oleifera* and *M. peregrina*, both readily available slender trees. With just one study examining a bottle tree species (Carlquist, 1998), the diversity of wood anatomical strategies in *Moringa* has been under-represented. Because trees with large quantities of water storage tissue are less familiar anatomically than more woody trees, special attention has been given to the marked diversity of water storage strategies observed in *Moringa*. Highlighted in particular is the polymorphism of libriform fibres, because these cells serve a variety of purposes from mechanical support to water and nutrient storage.

MATERIAL AND METHODS

Most samples were collected from living plants and preserved in locally available alcohol, usually 50–70% aqueous ethanol. Samples were transferred to 70% aqueous ethanol upon arrival at the Missouri Botanical Garden. Wood of *M. pygmaea* was obtained from herbarium specimens, boiled, and stored in ethanol. Voucher and locality information for samples is provided in Appendix 1. Recently fallen individuals of the largest species were found at most localities, so it was possible to collect samples of the main trunks of these trees without seriously damaging standing trees.

At least three individuals of each species were examined for determining the overall structural plan of the stem, and quantitative measurements were drawn from at least two individuals per species. The two exceptions are *M. pygmaea*, of which only two specimens were available, and *M. oleifera*, which is already well-documented (e.g. Durin, 1913; Metcalfe & Chalk, 1950). Sampling is summarized in Appendices 1 and 2. Strong differences between mature wood and wood of juvenile plants is observed in the stem and roots of many species of *Moringa*. Data in the present account are from the mature wood of large plants, that is, wood

away from the pith and at least a few mm from the cambium whenever possible.

The combination of very soft and very tough cells distributed throughout the stems and roots of *Moringa* made sectioning on a sliding microtome unsatisfactory. As a result, small stem or root chips were softened in 10% ethylenediamine for 1–3 days before being dehydrated and embedded in paraffin (method of Carlquist, 1982). Samples were sectioned on a rotary microtome at 13 µm and stained in a staining series corresponding to Northen's modification of Foster's ferric chloride-tannic acid staining series (Johansen, 1940), with the exception that ferric aluminum sulphate was substituted for ferric chloride. For scanning electron microscope (SEM) observation, paraffin sections were mounted on stubs using the same gelatin adhesive used for mounting the sections on glass slides. The paraffin was cleared with xylene and the samples sputter-coated and observed with a Bausch and Lomb Nanolab 200 SEM. Macerations were prepared using Jeffrey's solution (Johansen, 1940) and stained in safranin.

Vessel diameters are measurements of the lumen, because it is this space that is available for water conduction and therefore of greatest functional interest. In many cases, the vessels were oval in cross section, so either a chord was estimated that would reflect the area of the vessel, or the public domain program NIH Image (US National Institutes of Health; obtained at <http://rsb.info.nih.gov/nih-image/>) was used to calculate the vessel area from photomicrographs and then calculate a diameter for the vessel. In many cases both methods of measuring were used, with similar results. In either case, these figures represent idealized diameters that are used to infer the evolutionary responses of *Moringa* species to their habitats rather than purely descriptive devices.

To test for significant differences in quantitative measurements between habits, means of measurements from mature wood for each species were pooled to give a species mean for each characteristic measured. One-way ANOVAs were then used on each variable, followed by Tukey's HSD simultaneous pairwise mean comparisons (using SYSTAT for the Macintosh, v. 5.2) as a post-hoc test.

ABBREVIATIONS USED IN FIGURES

AP	axial parenchyma
B	bottom of Figure
C	centre of Figure
L	left-hand part of Figure
LF	libriform fibre
P	parenchyma
PP	paratracheal axial parenchyma
R	right-hand part of Figure

RS	radial section
TgS	tangential section
V	vessel
Ve	vessel element
VP	vasicentric axial parenchyma
XS	transection

Juvenile plants are shown in many of the habit plates. In all cases, the young plant is shown at twice life size relative to the 2 m tall person. The author of each species is cited in Figures 1–49.

RESULTS AND DISCUSSION

Quantitative measurements are presented in tabular form in Appendix 2. Qualitative characteristics of each species are summarized in Figures 1–52. Features that are common throughout the family are highlighted in Figures 61–66 and 92–111. Root transections are given in Figures 53–60. The structural and functional diversity of libriform fibres and axial parenchyma cells is illustrated in Figures 67–91. Significant differences and trends in the data are highlighted below.

HABITS IN *MORINGA* AND CORRELATIONS WITH ANATOMY

Based on gross appearance in the field, *Moringa* was divided into four habit classes: bottle trees, sarcorhizal trees, slender trees, and tuberous shrubs, described below. The bottle trees, slender trees, and tuberous shrubs display considerable within-class anatomical homogeneity. In contrast, the two species of sarcorhizal trees showed marked anatomical differences despite habitual similarity.

Moringa: four habit classes

(1) *Bottle trees* (*M. drouhardii*, *M. hildebrandtii*, *M. ovalifolia*, *M. stenopetala*; Figs 1–16) are characterized by massive trunks and swollen roots. The form of the trunk and roots are both similar, as is the bark colour and pattern of fissuring. Such bloated trees are also called 'tank trees' in reference to the large amounts of water stored in their swollen trunks. *Moringa hildebrandtii* is the largest member of the genus, commonly reaching 15 m and reported to reach 25 m (Keraudren, 1965). Trunk diameter of these species is commonly 60–100 cm but can exceed 2 m (e.g. plant on right in Fig. 9).

(2) *Sarcorhizal trees* (*M. arborea*, *M. ruspoliana*; Figs 17–24). Characterized by a more slender trunk than the bottle trees with tough, smooth bark and thick, soft, fleshy, somewhat contorted roots that differ markedly in appearance from the trunk, having paler bark that is much softer and with different patterns of fissuring from that of the stem.

(3) *Slender trees* (*M. concanensis*, *M. oleifera*, *M. peregrina*; Figs 25–36). The three principally Asian *Moringa* species have slender trunks at maturity and tough, fibrous roots with bark that is smoother, spongier, and more fragile than that of the stem. The root bark of all three species is less fissured than that of the very base of the stem.

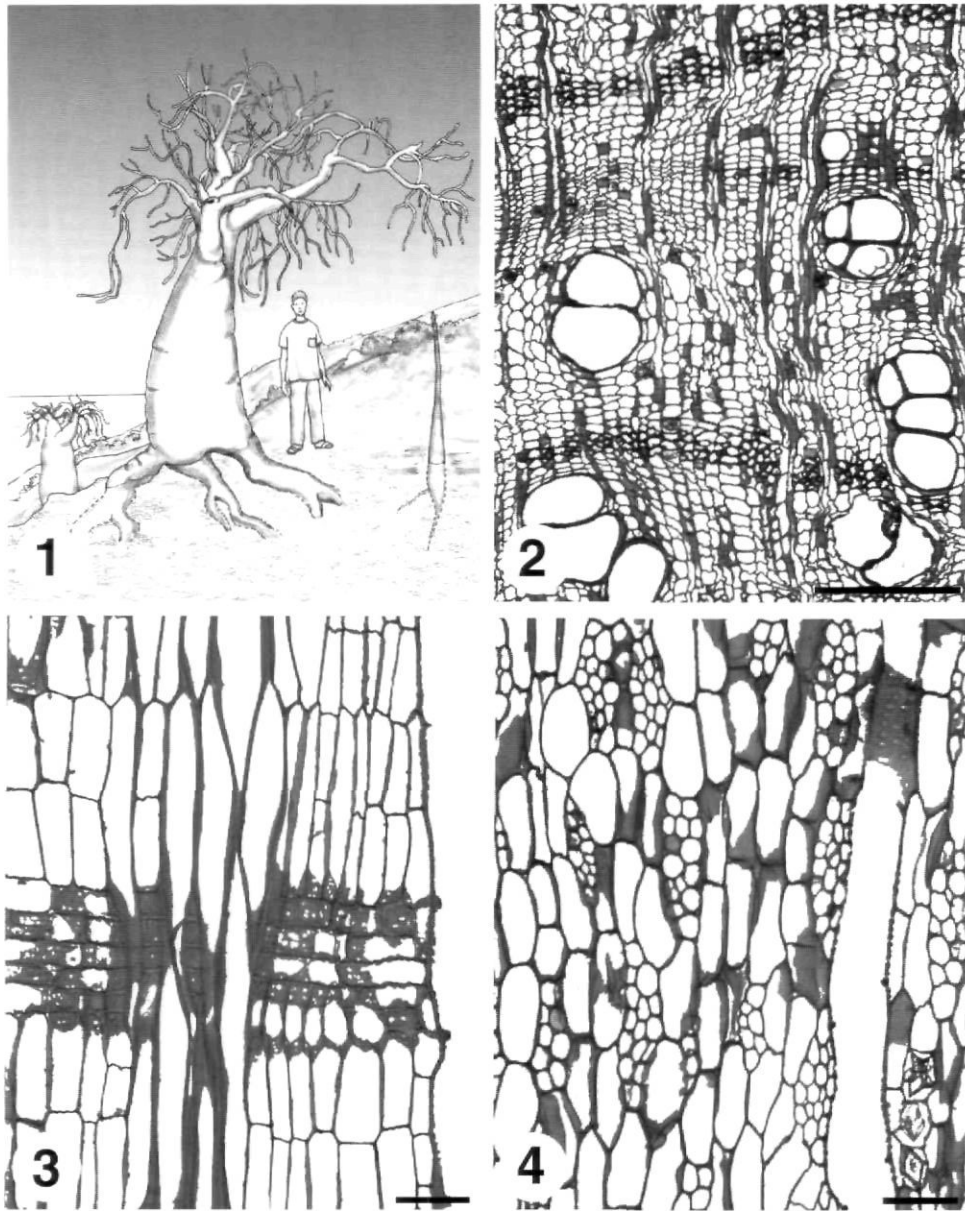
(4) *Tuberous shrubs* (*M. borziana*, *M. longituba*, *M. pygmaea*, *M. rivae*; Figs 37–52). Stems of three species are short-lived and persist only through favorable years, dying back to the large underground tuber during periods of extended drought. Only *M. rivae* is likely to form permanent shoots with age but nevertheless also has a very large, very soft tuber underground. The root is much greater in diameter than the stem, is much softer, and has softer, paler bark that is more prone to forming polygonal plates rather than longitudinal fissures.

Stem and root structural plan: arrangement of parenchyma and fibres

'Structural plan' as used here refers to the grouping of axial parenchyma and libriform fibres in the stem and root. Considerable variation in stem and root structural plan is associated with habit (summarized in Table 1).

Bottle trees. These are distinguished from other species of *Moringa* in having stems and roots that are not only similar in gross appearance, but are also similar in structural plan at the anatomical level. The stems of bottle trees all present the distinctive pattern of wide bands of confluent paratracheal axial parenchyma in earlywood, giving way often abruptly to bands of libriform fibres (Figs 2–16, especially as seen in transections, and Figs 76, 77), though in *M. stenopetala* these rings may be discontinuous. The structural plan of the secondary xylem of the roots is similar to that of the stem, and is composed mostly of wide bands of paratracheal axial parenchyma alternating with narrow bands of libriform fibres (Figs 53, 54).

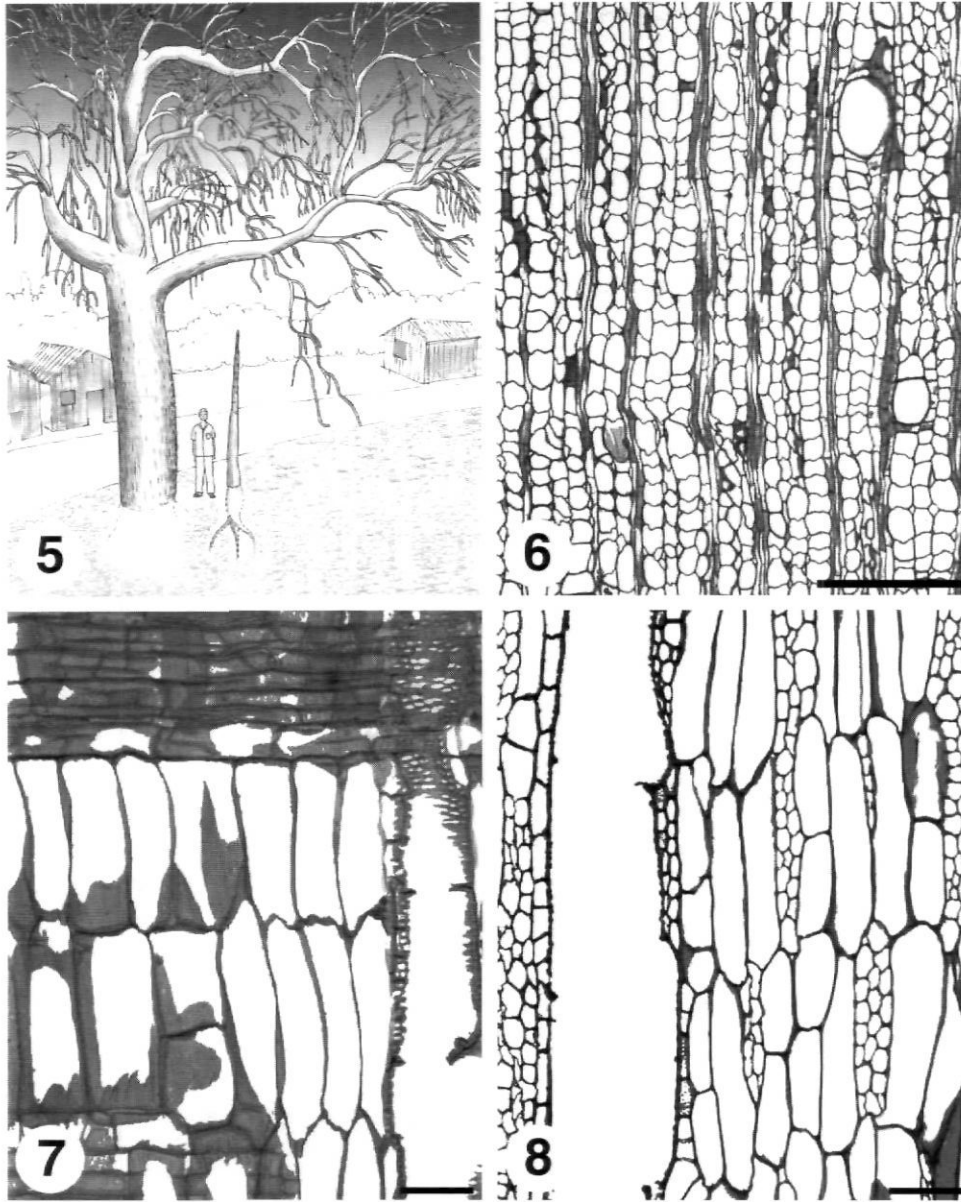
Sarcorhizal trees. Similarity between the two species in this habit class at the level of the whole plant belies differing shoot plans. In *M. arborea*, earlywood forms as a band of confluent aliform paratracheal parenchyma with few, usually short and wide, libriform fibres. Latewood is composed of mostly long, narrow libriform fibres (Figs 18, 19). As in *M. arborea*, wood of *M. ruspoliana* also shows bands of wide, water-storing cells alternating with bands of narrow libriform fibres serving chiefly as support structures (Figs 22, 23).



Figures 1-4. *Moringa drouhardii* Jum., habit and wood. Scale bar in Figures 2-4 = 100 μ m. Fig. 1. Habit; person is 2 m tall. Habitat of Olson 695. Fig. 2. XS Olson 679. Xylem composed of confluent bands of PP, with LF's restricted mostly to the darker arcs near top and bottom. Vascentric abundant P is conspicuous around the group of four Vs at upper R, one of which contains the remains of thin-walled tyloses. Fig. 3. RS Olson 696 showing a band of LF's of greatly varied length at C with parts of bands of PP on either side. V on R surrounded by a single layer of VP; division into strands usually more marked than shown here. Large pits can be seen in the mostly procumbent cells of the ray running across lower C. Fig. 4. TgS Olson 679 showing short, storied rays amid AP. V-P pitting can be seen on the V wall. Rhomboidal crystals and a druse can be seen in the small ray at lower R.

However, the water-storing cells of the stem of *M. ruspoliana* are short, very wide libriform fibres rather than axial parenchyma cells. Axial parenchyma in *M. ruspoliana* is limited to vascentric parenchyma surrounding vessels in a layer a single cell thick. In

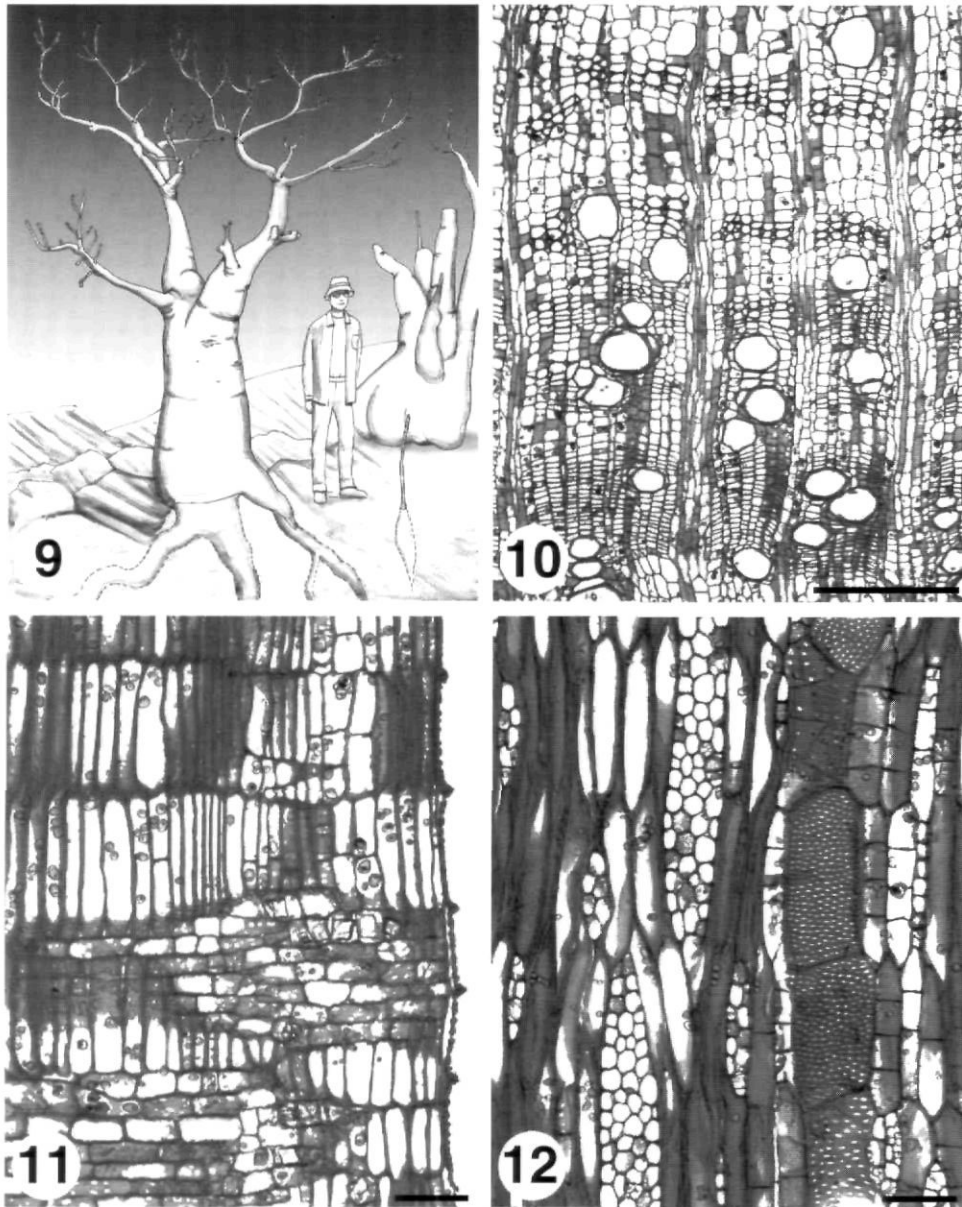
contrast, the roots of *M. arborea* and *M. ruspoliana* have nearly indistinguishable plans. The roots of both species are characterized by wide bands of irregularly-sized paratracheal axial parenchyma and occasional bands of libriform fibres (Fig. 55).



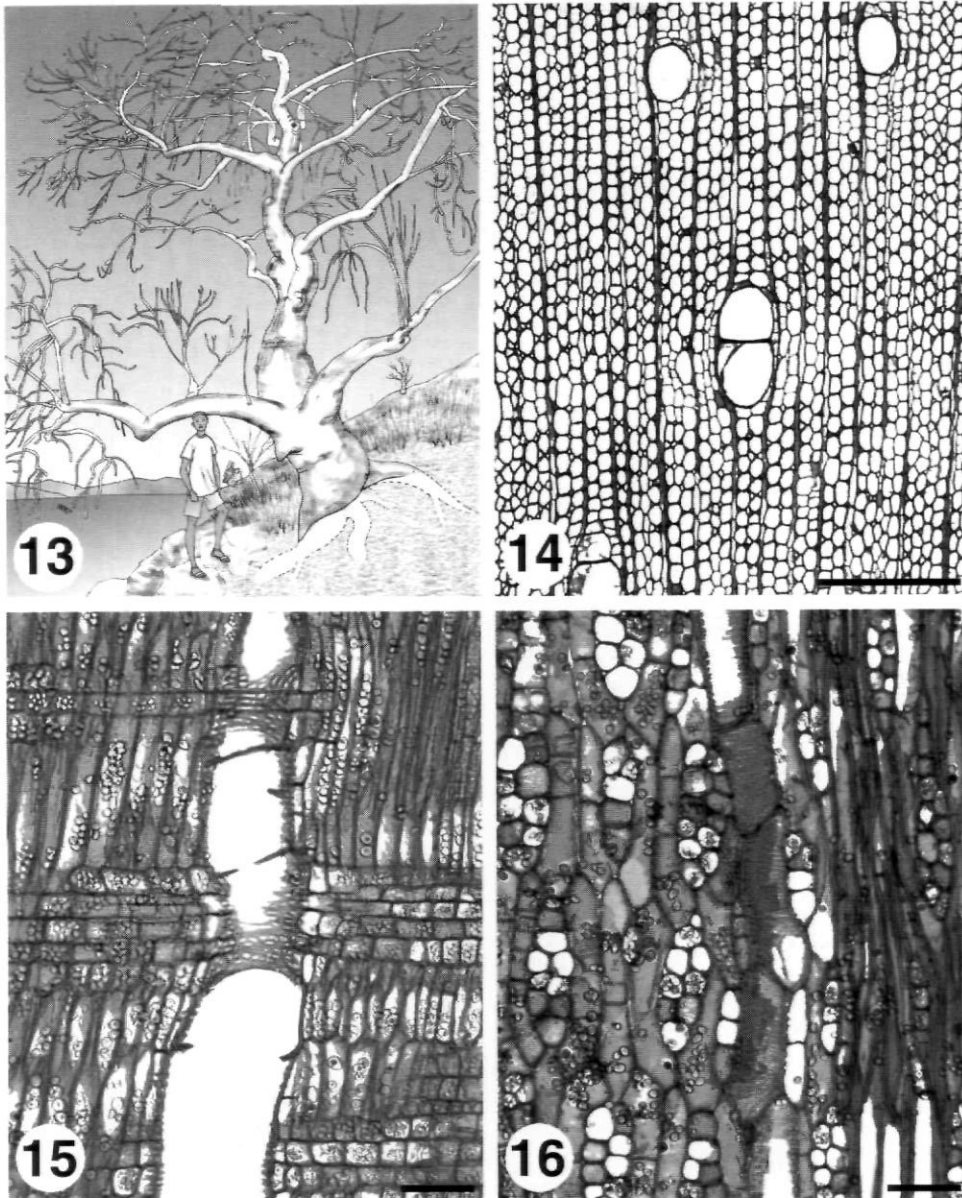
Figures 5–8. *Moringa hildebrandtii* Engl., habit and wood. Scale bar in 6 = 500 μm , in 7 and 8 = 100 μm . Fig. 5. Habit; person is 2 m tall. The species is always found in association with people, and wild localities have never been documented. Figures 6–7. Olson 693. Fig. 6. XS showing large cell diameters given over to water storage. LFs can be similar in appearance to AP in XS; the short tails of some LFs can be seen just above the '6' Fig. label. Fig. 7. RS showing earlywood P on L and short, wide latewood LFs to the R. The V begins another ring of earlywood. A small amount of VP divided into strands is to L of the V just below the ray. V-ray pitting and a small amount of V-VP pitting are shown. Fig. 8. TgS Olson 697 showing vaguely storied rays and AP. VP visible on L side of the V.

Slender trees. Stems are characterized by a preponderance of libriform fibres that show little seasonal variation in shape with little axial parenchyma, though this pattern does show some variation. In favorable seasons, *M. concanensis* earlywood libriform fibres are sometimes replaced by confluent aliform paratracheal parenchyma, less commonly so in *M. peregrina* and *M. oleifera*.

As in the other arboreal life forms, the root secondary xylem of the slender trees shows alternating bands of libriform fibres and paratracheal axial parenchyma. However, in the slender trees, the parenchyma bands are never wider than adjacent bands of fibres as they are in the other arboreal species (Figs 57, 58). This predominance of libriform fibres make the roots of the slender trees the toughest in the genus.



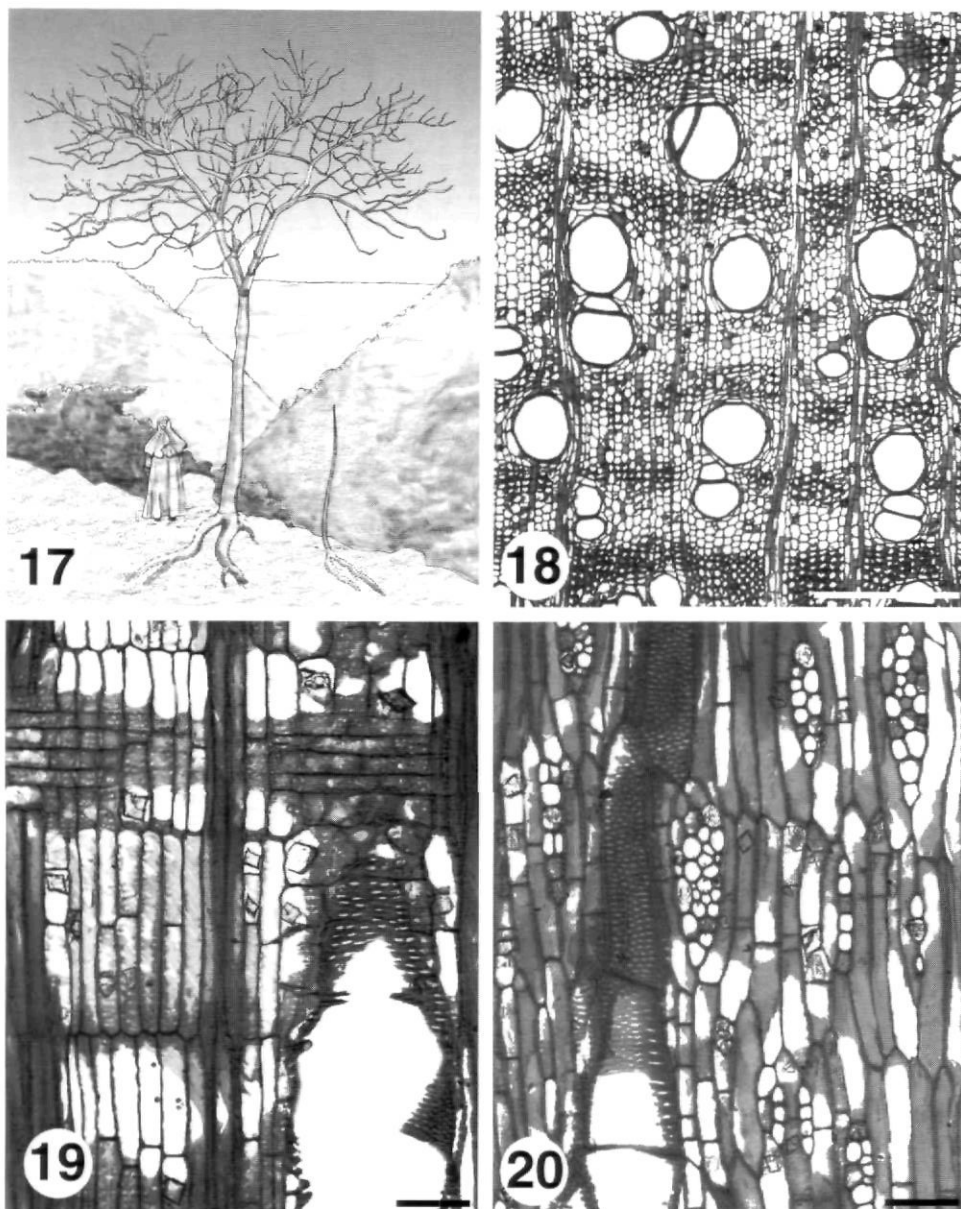
Figures 9–12. *Moringa ovalifolia* Dinter & A. Berger, habit and wood Olson 718. Scale bar in 10 = 500 μm , in 11 and 12 = 100 μm . Fig. 9. Habit; person is 2 m tall. Young plant on lower R. Individual subject to elephant disturbance on R, undisturbed individual at C. Fig. 10. XS showing much narrower growth rings and smaller cells than other bottle trees, a reflection of the more arid habitat of this species. However, structural plan is similar with water storage undertaken by both AP and P-like LFs. The distinction is clear at top, showing a dark band of LFs surrounded on either side by PP, probably produced in a season of abundant rainfall. The rings at B, which are very thin and composed exclusively of AP, are likely associated with lower rainfall. Fig. 11. RS showing LFs on the extreme L. To the R of these LFs is a band of wide, truncate AP cells. The narrower cells at C are LFs that do not appear very distinct from the P cells. AP fills the area between this band of LFs and the V on the R. Starch is abundant in both P and LFs, and rhomboidal crystals and a druse can be seen in the ray cells. Fig. 12. TgS through a band of more typical LFs. VP can be seen adjacent to the V on the R; as on the far R, AP cells adjacent to rays sometimes divide into strands. The lowermost Ve and the uppermost one that can be seen in its entirety show V-VP pitting. V-V pitting can be seen on the two middle Ves.



Figures 13–16. *Moringa stenopetala* (Baker f.) Cufod., habit and wood, Olson 675. Scale bar in 14 = 500 μm , in 15 and 16 = 100 μm . Fig. 13. Habit; person is 2 m tall. Habitat of Olson 675. Fig. 14. XS with Vs surrounded by aliform bands of AP separating irregular bands of LFs that are difficult to distinguish from the P cells in XS. Four such zones of LFs are included in this section, one of which runs above the V at C. Fig. 15. RS showing several layers of AP on both sides of the V and LFs at either side of the micrograph. V-ray pitting is visible on V walls. Starch is abundant in P, LFs, and ray cells. Fig. 16. TgS. Storied rays and AP to the L of the V, with AP cells adjacent to rays often subdivided. LFs on far R. V-V pitting on V walls at C.

Tuberous shrubs. Though their stems are much thinner than those of the slender trees, the tuberous shrubs show analogous variation in plan. All four species are characterized by a preponderance of libriform fibres. Only vascentric axial parenchyma was observed in *Moringa longituba* and *M. pygmaea*, whereas *M. borziana* and *M. rivae* may facultatively produce early-

wood bands of paratracheal axial parenchyma. Despite the variation in size of these species and that *M. rivae* can form permanent stems, great uniformity of structural plan is seen at the root level in this habit class. Secondary xylem of the tubers is formed almost entirely of axial parenchyma, often in radial files, with an apparent absence of libriform fibres (Figs 59, 60).

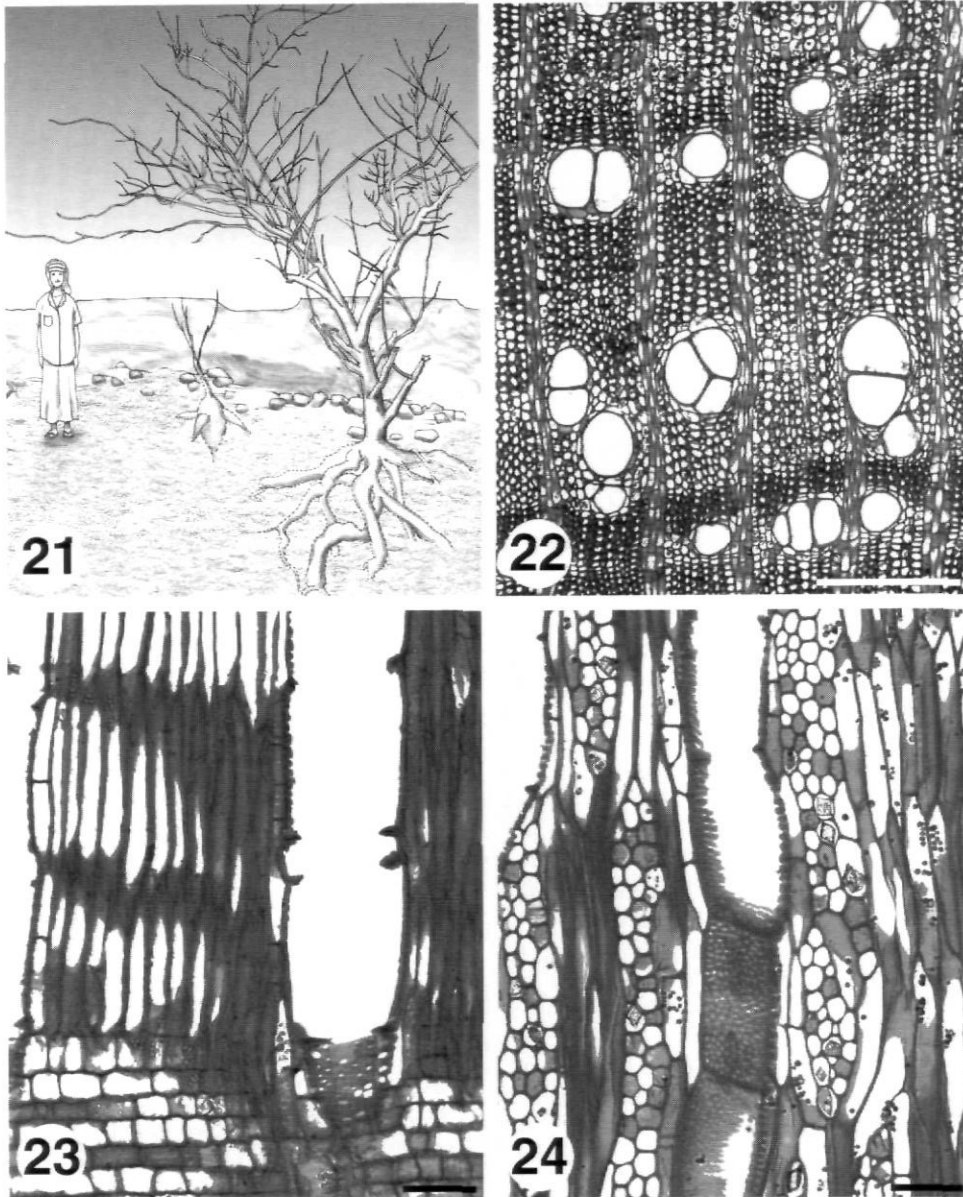


Figures 17–20. *Moringa arborea* Verdc., habit and wood, Olson 714. Scale bar in 18 = 500 μm , in 19 and 20 = 100 μm . Fig. 17. Habit tall, slender trunk with divaricating crown and few, fleshy, soft roots; person is 2 m tall. Only known locality is a rocky canyon in a low limestone mesa. Fig. 18. XS with dark bands of LFs alternating with lighter bands of AP in which most of the Vs occur. End walls are commonly seen in the AP. Note the interruption of the band of LFs by AP surrounding the two groups of Vs at bottom R and C. Fig. 19. RS. Thin bands of LFs can be seen as long, dark cells with elongate, acute tails on the extreme L and at C, with part of another such band on the extreme R. AP are wider cells with truncate end walls that often include rhomboidal crystals. A small amount of VP, divided into strands, adjacent to the L of the V toward B. V-AP pitting on the Ve wall, and predominantly procumbent cells can be seen in the ray that crosses the upper third of the micrograph. Fig. 20. TgS through a band of AP showing V-V pitting and abundant druses and rhomboidal crystals in AP and ray cells. VP can be seen in two layers along the lower half of the V.

Vessel elements

Qualitative characteristics of vessel elements remain fairly constant throughout the family (Figs 61–66 and 92–94) but show distinct quantitative trends (Appendix

2). The tuberous shrubs have shorter, narrower vessel elements with thinner walls than the other life forms. Vessel element dimensions show similarity between the sarcorrhizal trees and the tuberous shrubs despite



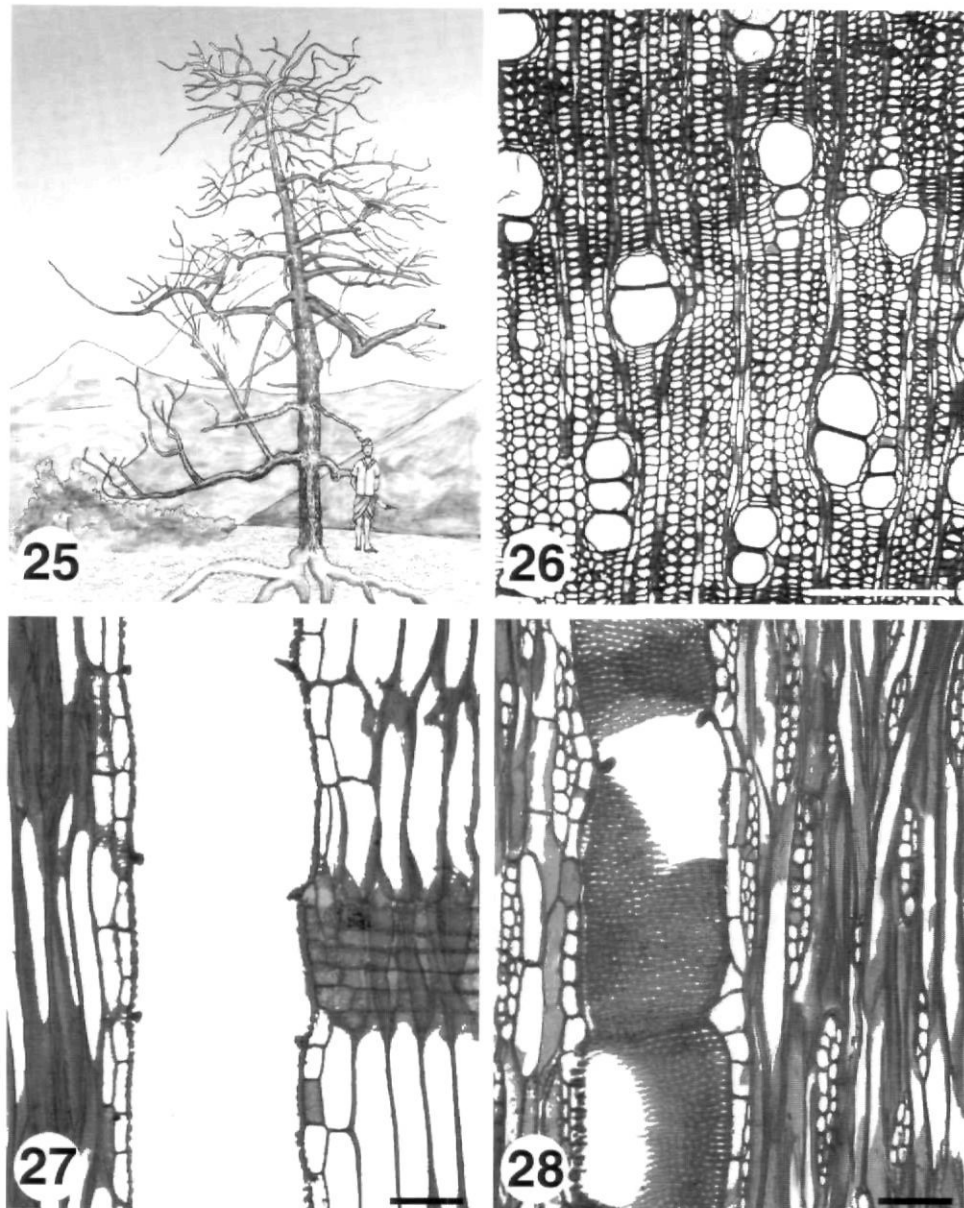
Figures 21–24. *Moringa ruspoliana* Engl., habit and wood. Scale bar in 22 = 500 μm , in 23 and 24 \approx 100 μm . Fig. 21. Habit. Branched crown from low trunk(s) with abundant very fleshy roots; person is 2 m tall. Young plant with turbiniform tuber. Fig. 22. XS Olson 702. AP is confined to 1–2 layers VP. The banded appearance of the wood in XS is due to rings of wide, short LF's (visible around Vs) alternating with bands of long, narrow ones (e.g. above bottom Vs). Figures 23, 24. Olson 703. Fig. 23. RS showing a single layer of VP around the Vs. Narrow LF's to the R of the R V, wider LF's between the Vs. V-AP pitting on V wall. Fig. 24. TgS showing wide, tall rays with rhomboidal crystals. Narrow LF's on L, wider LF's on R. V-V pitting on V walls.

the size difference between the members of these classes. Vessel element diameter is significantly smaller in tuberous shrubs than in bottle trees or slender trees, but not from the sarcorrhizal trees. Likewise, vessel density and conductive area are much closer between the sarcorrhizal trees and the tuberous shrubs than between the other life forms. Vessels in bottle trees are the widest in the family, but are surrounded

by large expanses of parenchyma. As a result, members of this life form tend to have fewer vessels per group than the other life forms and lower vessel density.

Imperforate tracheary elements: polymorphism in size and shape

Libriform fibres show marked variation in size and in the patterns of variation in shape between life forms.

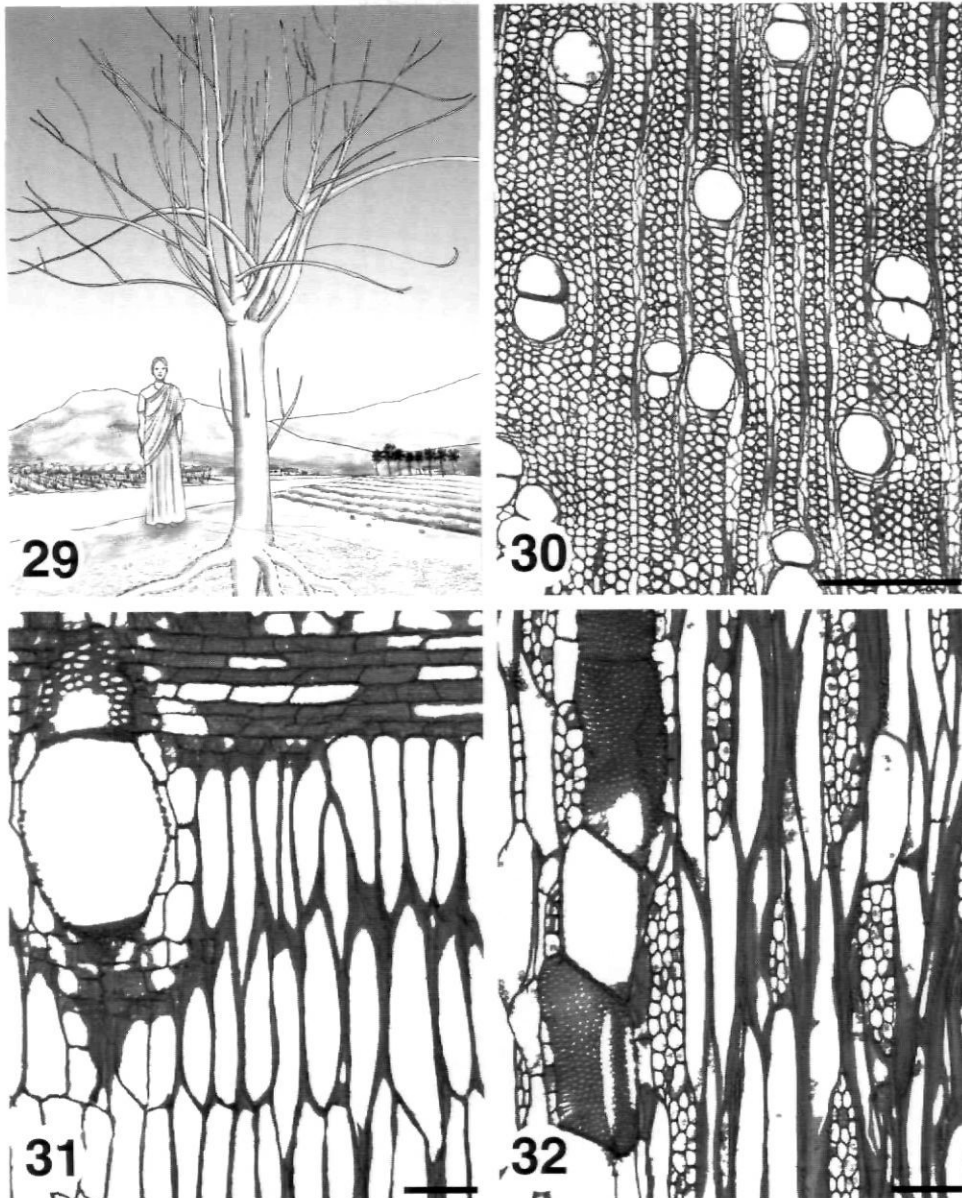


Figures 25–28. *Moringa concanensis* Nimmo, habit and wood, Olson 700. Scale bar in 26 = 500 μm , in 27 and 28 = 100 μm . Fig. 25. Habit showing strong main trunk with deeply furrowed bark and tough, spreading roots; person is 2 m tall. Fig. 26. XS showing Vs in lower half of micrograph surrounded by often confluent bands of aliform PP replacing LFs in earlywood. AP in upper half mostly limited to 1–2 layers VP with LFs predominating. Fig. 27. RS. V with 2 layers VP, wide earlywood LFs to R and narrow latewood LFs to L. Fig. 28. TgS with AP to L of V, one layer of VP on R. LFs on R with vaguely storied rays. V-V pitting on V walls.

As used here, 'size' refers to measurements of fibre length, diameter, or wall thickness, considered independently of one another. 'Shape' refers to the length and diameter of a given fibre considered together, which roughly describes the overall form of a fibre. Libriform fibre 'type' in the following discussion refers to the figure number corresponding to the different fibres depicted in Figures 67–75.

With regard to size, *Moringa* shows a clear trend in

fibre length, with the largest life form (the bottle trees) having the longest fibres, followed by the sarcorhizal trees, then the slender trees, and the smallest species (the tuberous shrubs) having the shortest. As with vessel diameter, fibre diameters of the sarcorhizal trees and the tuberous shrubs are not significantly different. On the other hand, there is a significant difference between the diameters of fibres in tuberous shrubs *vs* bottle trees and a difference verging on being sig-

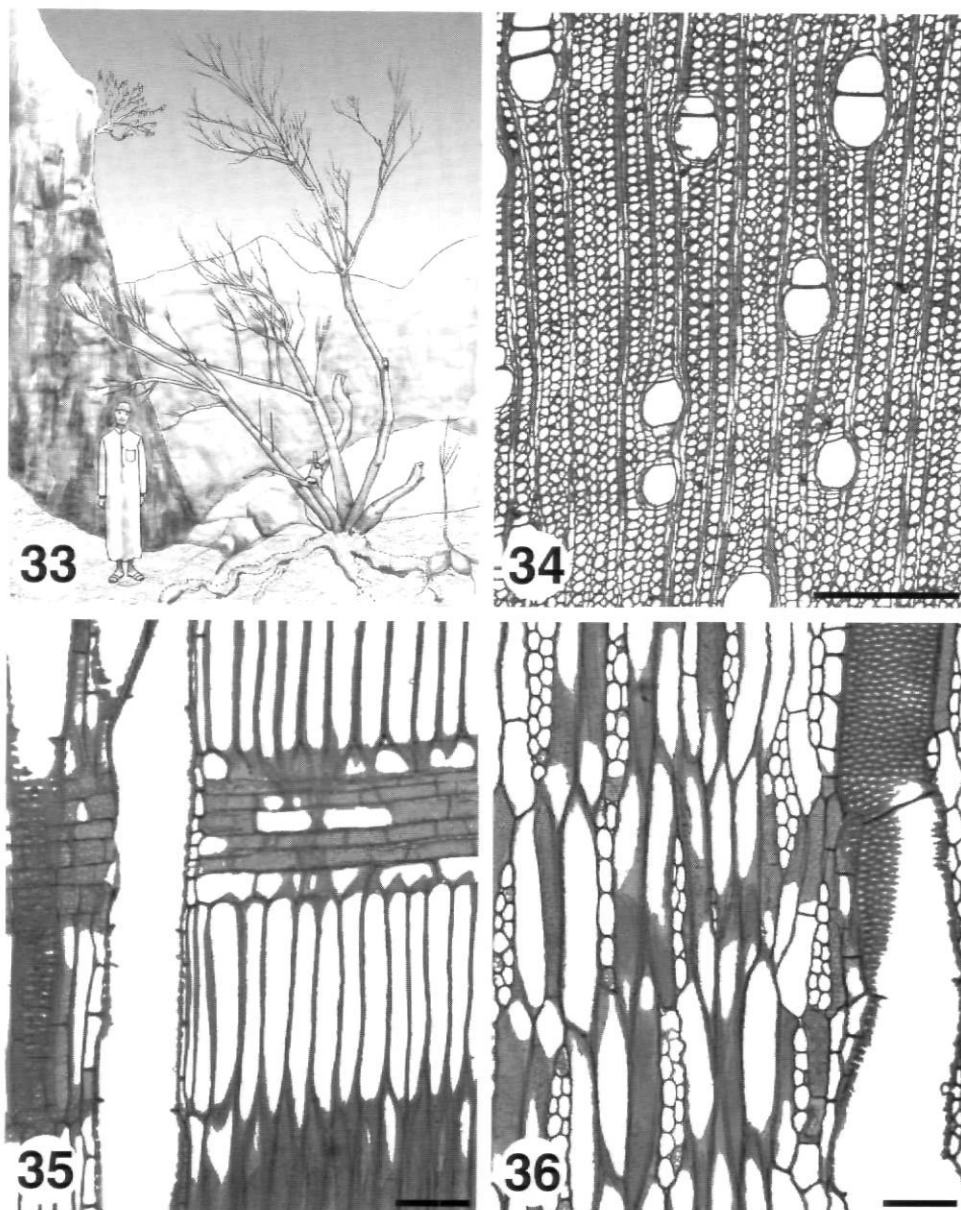


Figures 29–32. *Moringa oleifera* Lam., habit and wood, Olson s.n. Scale bar in 30 = 500 μm , in 31 and 32 = 100 μm . Fig. 29. Habit; person is 2 m tall. A field of the annual cultivar PKM ('bush moringa') on L. Fig. 30. XS showing variety of LF shape arranged without conspicuous banding. AP limited to 1–2 layers VP. Vs apparently in diagonal rows. Fig. 31. RS showing relatively uniformly-shaped LFs and VP around V. V-ray pitting on V wall. Fig. 32. TgS. LFs abundant, AP limited to VP adjacent to V at top. Rays somewhat storied. V-V pitting on V wall.

nificantly narrower than the fibres of the slender trees ($P=0.051$). The slender trees and tuberous shrubs tend to have slightly thicker-walled libriform fibres than the stems of the bottle and sarcorhizal trees, which have a greater quantity of thin-walled, water-storing fibres.

From sections, the distinction between bands of long, slender fibres and short, wide ones often seems very obvious (e.g. in transection in Fig. 22 and in radial section in Fig. 76), giving the impression of marked

fibre dimorphism. However, in macerations, a great breadth of fibre shapes is seen spanning the entire range from long and narrow to short and wide. This variation is depicted in scatterplots showing the distribution of length *vs* diameter measurements for 100 fibres per sample (Figs 79–91), which provide a ready way of visualizing the distribution of fibre shapes found within a given species. Points in the upper left of the plots represent very long, narrow fibres; points in the lower right represent very short, wide fibres; points in

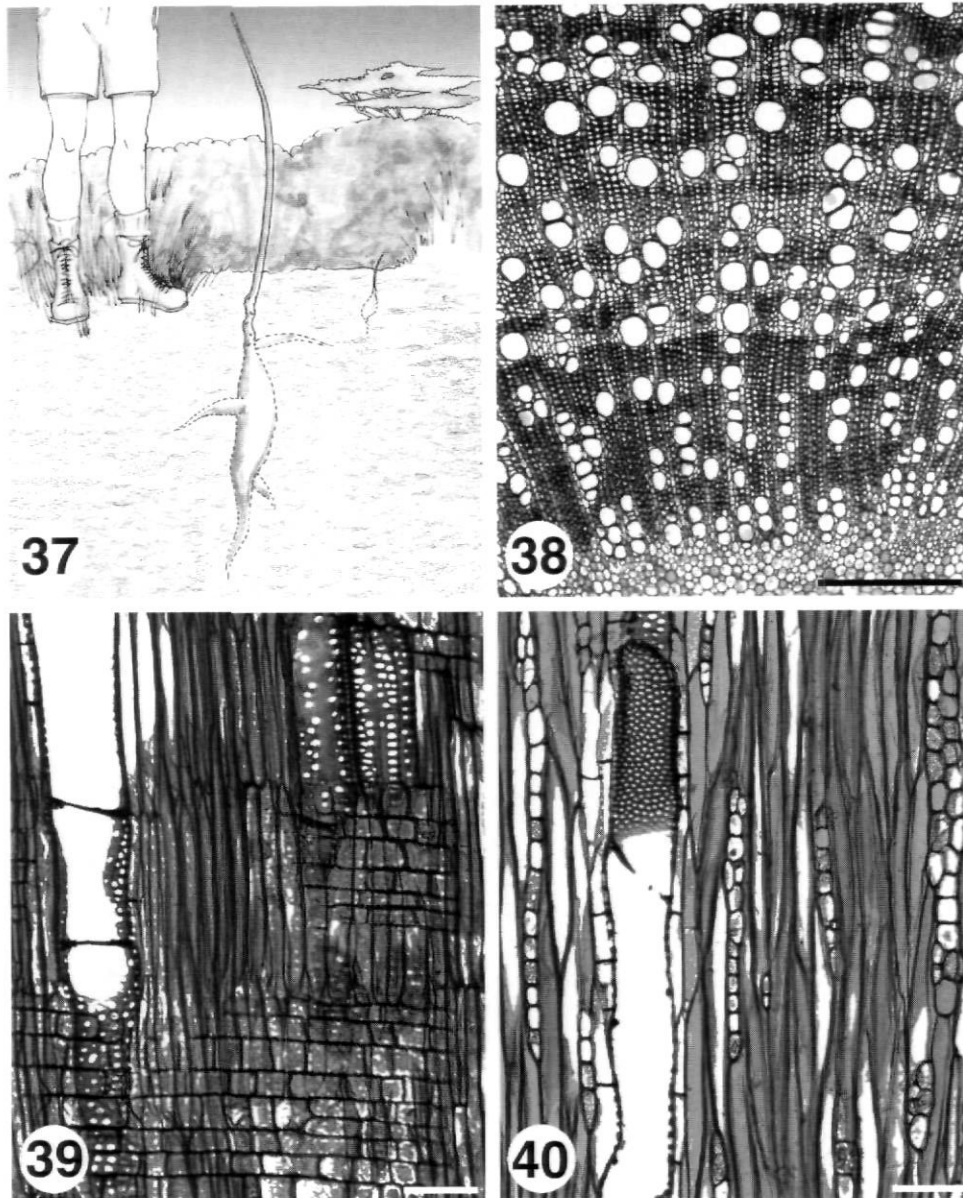


Figures 33–36. *Moringa peregrina* (Forssk.) Fiori, habit and wood, Olson 567. Scale bar in 34 = 500 μm , in 35 and 36 = 100 μm . Fig. 33. Habit; person is 2 m tall. *M. peregrina* often grows at the bottom of dry washes or on the walls of rocky canyons. Fig. 34. XS showing abundant LFs with AP confined to 1–2 layers VP. Fig. 35. RS showing lack of banding of differently-shaped LFs. VP divided into strands on lower L of R V. V-AP pitting on L V. Fig. 36. TgS showing storied rays and LFs, V-V pitting on V walls.

the lower left represent fibres that are short and narrow. Because one dot on the scatterplot can represent more than one cell, an ellipse encircling 50% of the data is included on each plot to highlight the tendencies in shape variation of each species.

Variation within the habit classes can be summarized as follows:

Bottle trees. These produce a wide range of fibre shapes, from very long and narrow fibre cells that provide mechanical strength, to short, wide fibres that serve a parenchyma-like function, storing water and starch. This diversity is manifested in the scatterplots in Figures 79–84 by the points and ellipse angling from upper left to lower right. Variation in fibre shape



Figures 37–40. *Moringa borziana* Mattei, habit and wood, Olson 678. Scale bar in 38 = 500 μm , in 39 and 40 = 100 μm . Fig. 37. Habit very large tuber underground and small shoot; person is 2 m tall. Shoots persist for few seasons. Fig. 38. XS showing seasonal variation in LF diameter. LFs predominate in the wood, comprising the darker bands. In some cases, as in the upper half of the micrograph, earlywood LFs are replaced by bands of PP. Fig. 39. RS illustrating preponderance of LFs. V-ray pitting at lower L similar in shape to V-AP pitting at upper R. Abundant large pits visible on ray cells. Fig. 40. TgS showing 2 layers of VP, abundant LFs of similar shape, and the often tall rays.

within seasonal bands is common in the form of short, wide fibres occurring at the end of the earlywood parenchyma (corresponding to the types in Figs 71–73), and progressively longer and narrower fibres being produced through the end of the latewood (the types in Figs 74, 75; visible in RS in Figs 11 and 76). *Moringa drouhardii* is distinguished from the other bottle trees in having fewer parenchymalike fibres than the other bottle trees. Storage in this species is performed mostly

by axial parenchyma cells, and most of the fibres produced are of the narrow support type (usually resembling the type in Fig. 75, sometimes grading to that depicted in Fig. 74). Variation in libriform fibre shape distribution in bottle trees is illustrated in Figures 76–78.

Sarcorhizal trees. The two species show different patterns of fibre shape distribution that correspond to

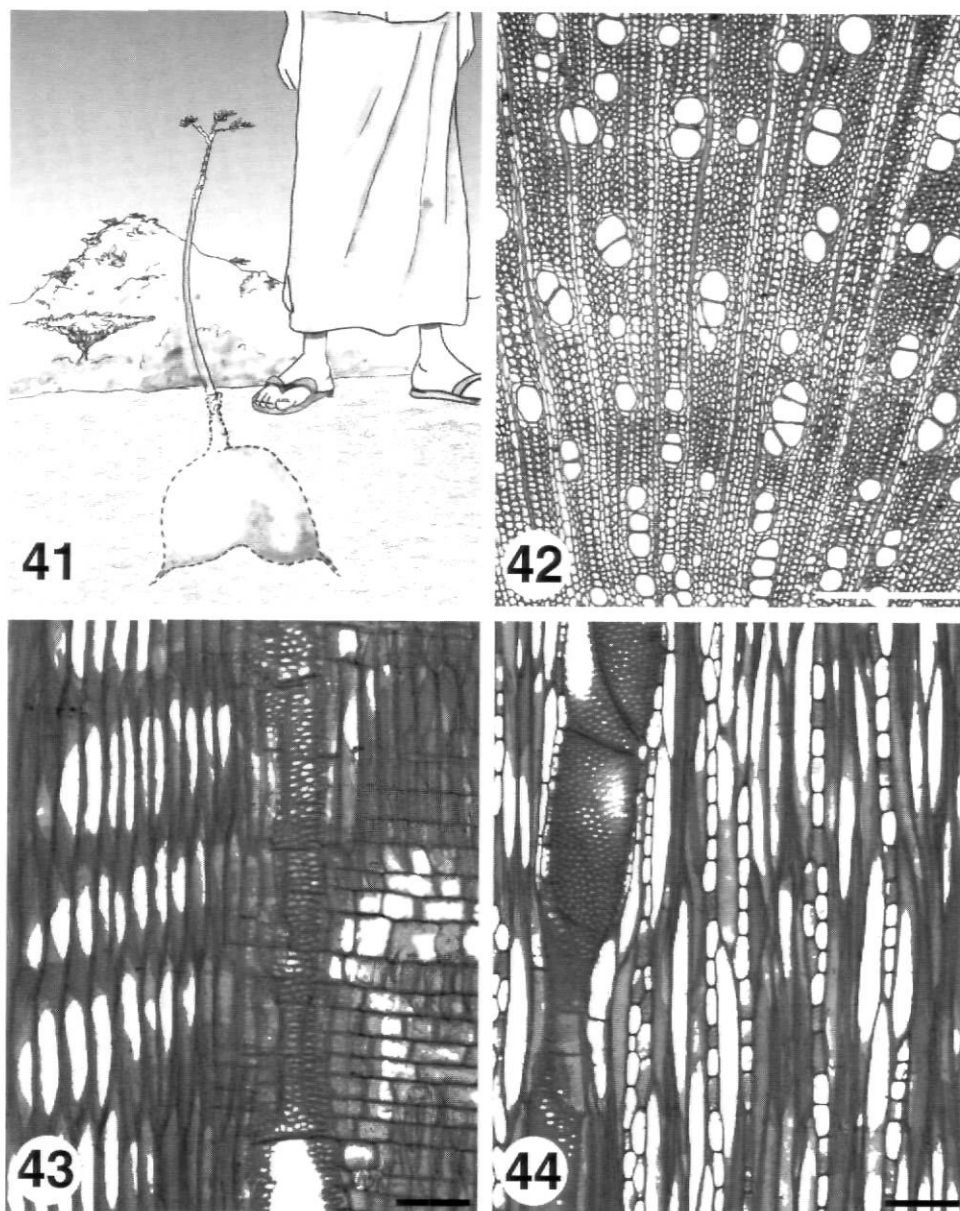
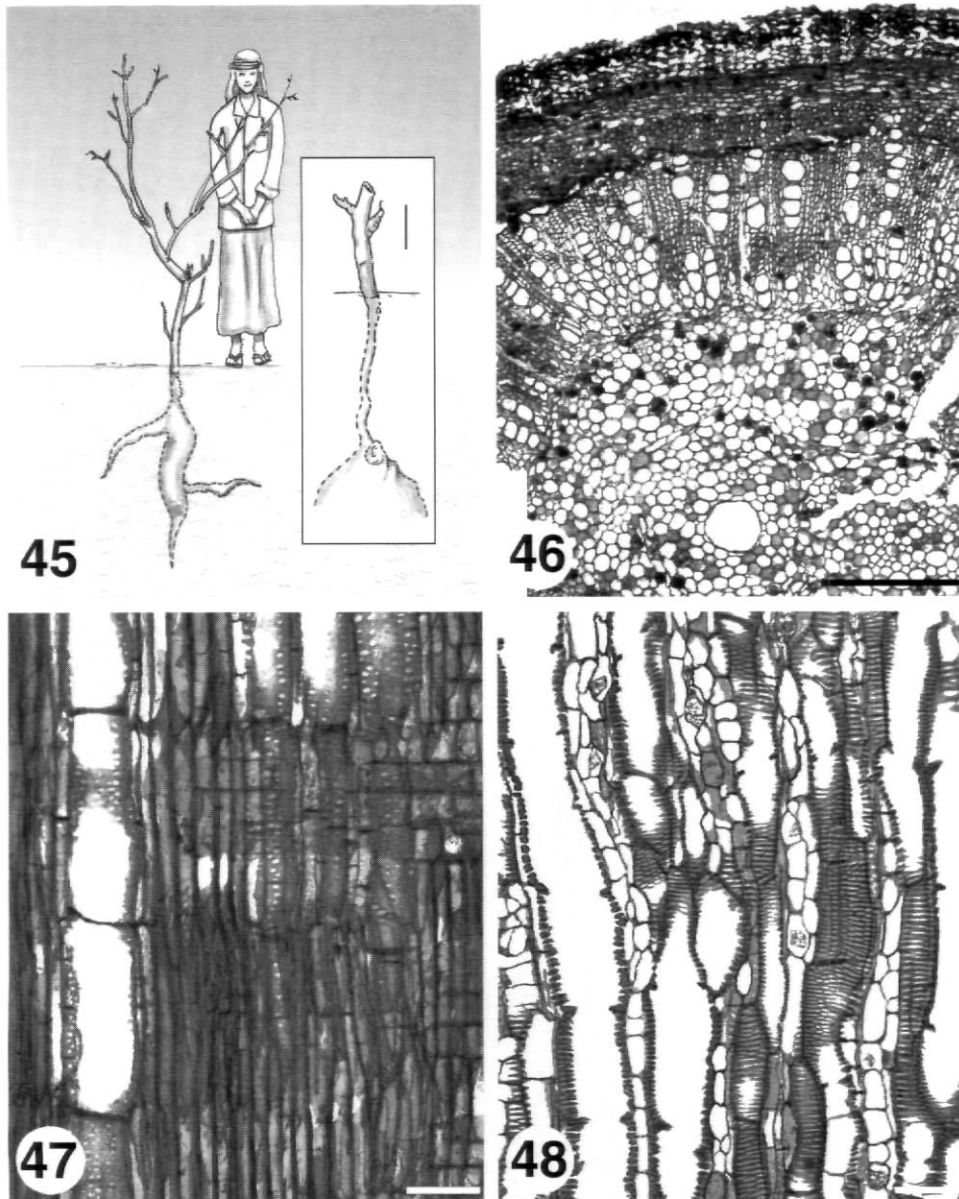


Figure 41–44. *Moringa longituba* Engl., habit and wood, Olson 704. Scale bar in 42 = 500 μm , in 43 and 44 = 100 μm . Fig. 41. Habit of plant in exposed sites usually short-lived shoot from large tuber far underground. When growing under other plants, *M. longituba* often scrambles to 3 m; person is 2 m tall. Fig. 42. XS to illustrate lack of conspicuous banding of LFs or AP and the preponderance of narrow fusiform LFs; LFs sometimes slightly larger at beginning of season. Fig. 43. RS showing lack of banding, V-VP pitting along length of V. Rhomboidal crystals common in ray cells but druses absent. Fig. 44. TgS showing fusiform shape of LFs, very tall rays, small amounts of VP along the V. V-VP just above figure label '44', and V-V pitting at top of V.

differences in stem plan. *Moringa arborea* relies on axial parenchyma for storage and has fibres that apparently serve mainly in support and tend to be fairly similar in diameter (types 74, 75; Figs 19, 83). In contrast, libriform fibres in *M. ruspoliana* span the entire range of shape and function seen in the family. Earlywood fibres are short and wide (types 71–73, visible between the vessels in Fig. 23), storing water

and starch in a parenchyma-like role. Latewood fibres are long and slender (as in Figs 74, 75, on extreme right of Fig. 23), and serve chiefly in support, a function more characteristic of libriform fibres. The inclined scatterplot in Figure 84 reflects this diversity of form.

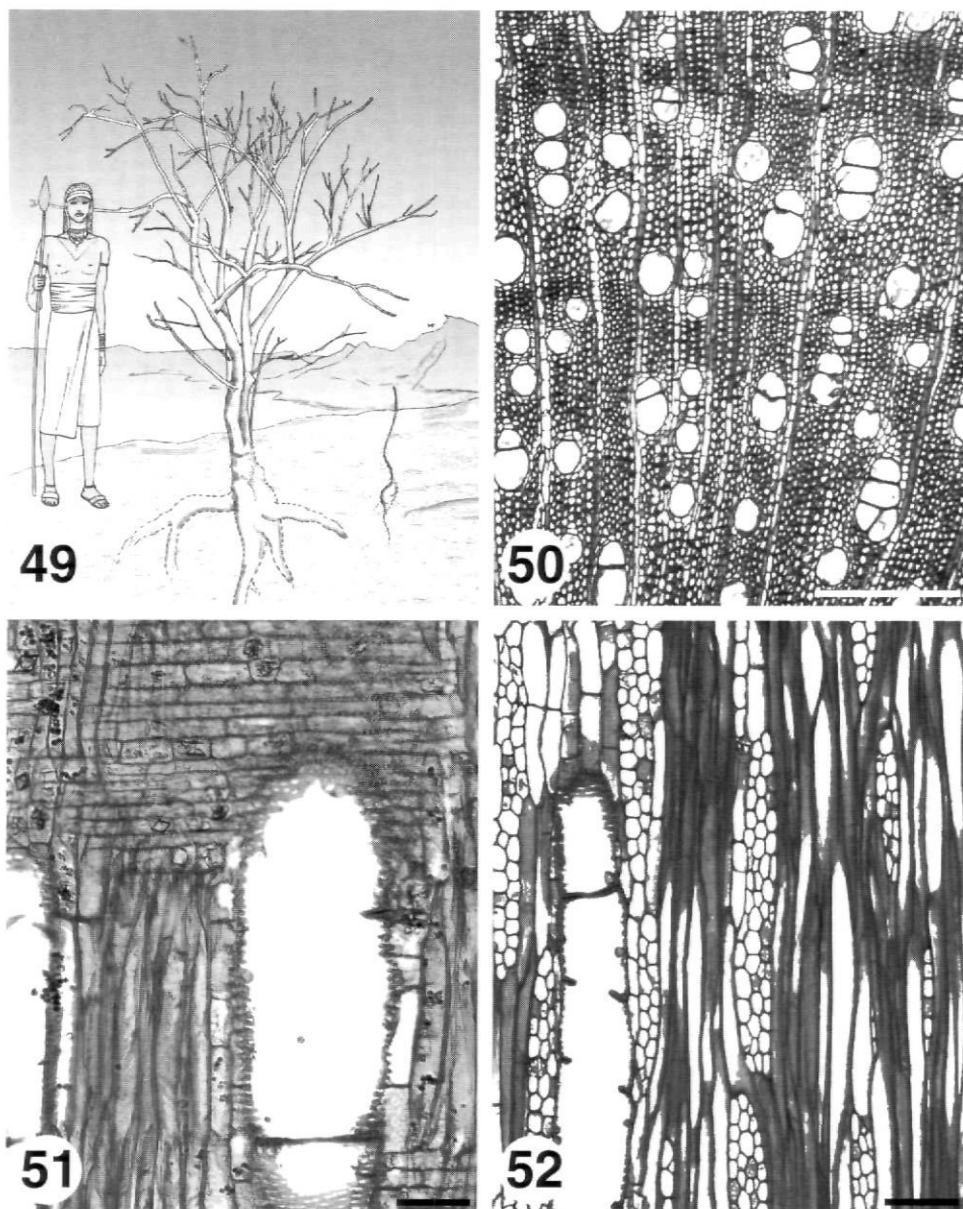
Slender trees. In trans- and radial sections, fibres of different shape in slender trees do not appear to occur



Figures 45–48. *Moringa pygmaea* Verdc., habit and wood. Scale bar in 46 = 500 μm , in 47 and 48 = 100 μm . Fig. 45. Habit of Glover and Gilliland 1194 based on description on specimen label; person is 2 m tall. Inset: drawing of the stem from the type specimen, Nugent 25; tuber is artist's addition. Scale bar = 3 cm. Fig. 46. XS of stem of Nugent 25 showing abundant Vs and LFs in the very thin xylem cylinder and gum duct in pith. Fig. 47. RS of Glover and Gilliland 1194, showing preponderance of elongately fusiform LFs. V-VP pitting on all V walls. Fig. 48. TgS of stem of Nugent 25 showing abundant Vs and rays and occasional cells of VP. V-V pitting, as at R of C, alternate to nearly scalariform. Druses and rhomboidal crystals abundant in ray cells.

in marked bands as in most of the other arboreal species, nor to vary with season with any regularity. Instead, the various shapes of libriform fibres are distributed homogeneously throughout the stem rather than in bands (though the fibres may be in rings separated by aliform to confluent aliform parenchyma, e.g. Fig. 26). The scatterplots in Figures 85–87 show the broad range of fibre shapes in the slender trees.

The ranges of shapes may be as great as those in the bottle trees, but the distribution of these shapes is less strongly orientated from long and narrow to short and wide (diagonally on the plots from upper left to lower right). Instead, the distribution is more diffuse and the ellipse broader with a weaker tendency for short cells to be wider than tall ones. A variety of co-occurring shapes can be seen in the longisections in Figures 31–36.



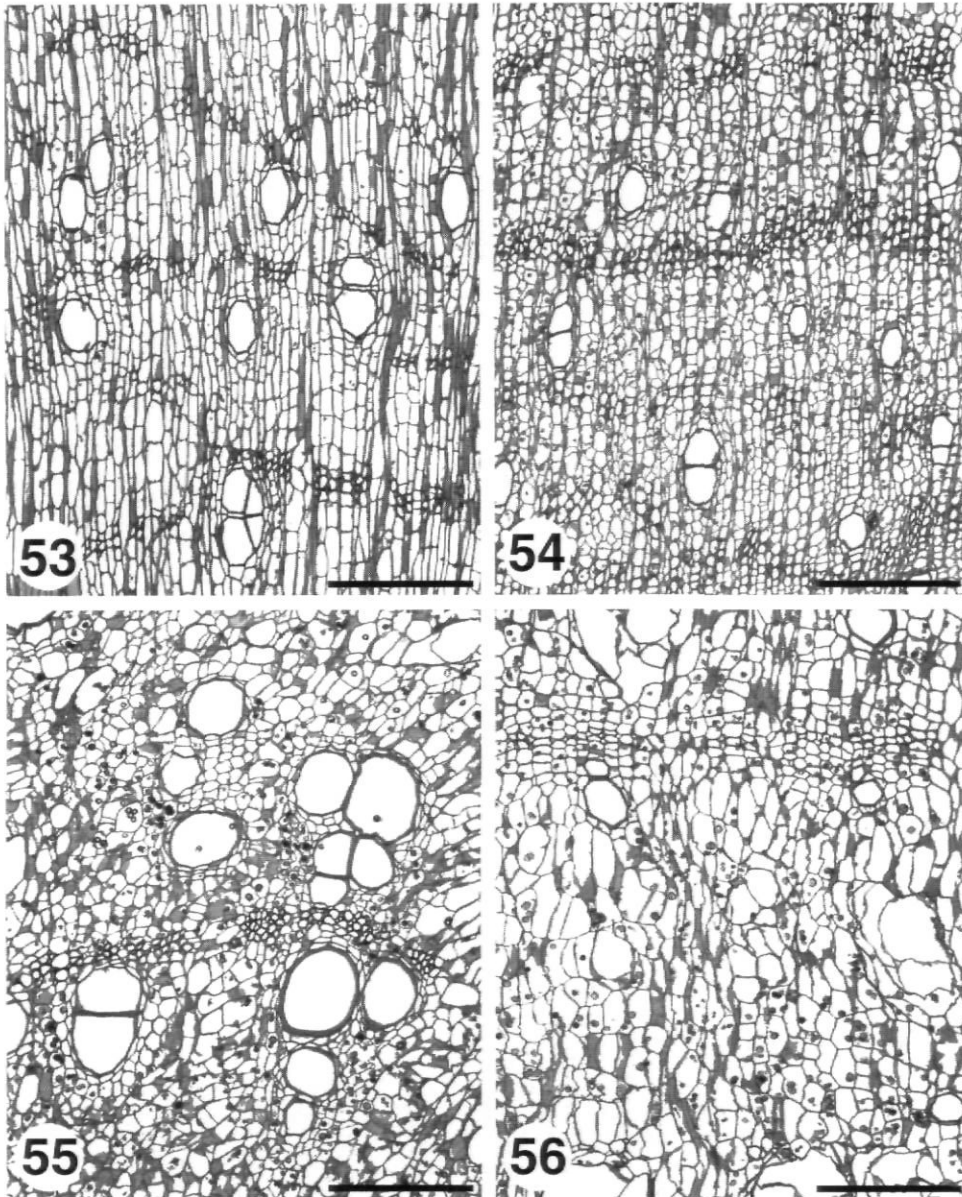
Figures 49–52. *Moringa rivaе* Chiov., habit and wood. Scale bar in 50 = 500 μm , in 51 and 52 = 100 μm . Fig. 49. Habit of Olson 677; person is 2 m tall. Fig. 50. XS Olson 677. Seasonal variation in LF size visible; earlywood sometimes replaced by PP (not shown). In this image, AP is present only in a single layer of VP. Fig. 51. RS Olson 701 showing some variation in LF size, with wider LFs at R and narrower ones at C. V surrounded by VP. Starch abundant in LFs, particularly those close to the V. Fig. 52. TgS of Olson 701 showing lack of variation in LF shape, rays that are often storied or very tall. VP above V.

Tuberous shrubs. Although some variation in size associated with seasonal changes is often observed in tuberous shrubs (e.g. Fig. 38), the fibres in these species are functionally similar and show less variation in diameter than do those of the arboreal species. Tuberous shrubs produce narrow libriform fibres that are usually of intermediate length and never produce wide, parenchyma-like fibres. The nearly vertical ellipses in

Figures 88–91 illustrate this tendency to vary widely in length but little in diameter.

Rays

Rays differ among the life forms mainly in size and proportion of upright to square to procumbent cells. The shortest multiserial rays were found in the slen-



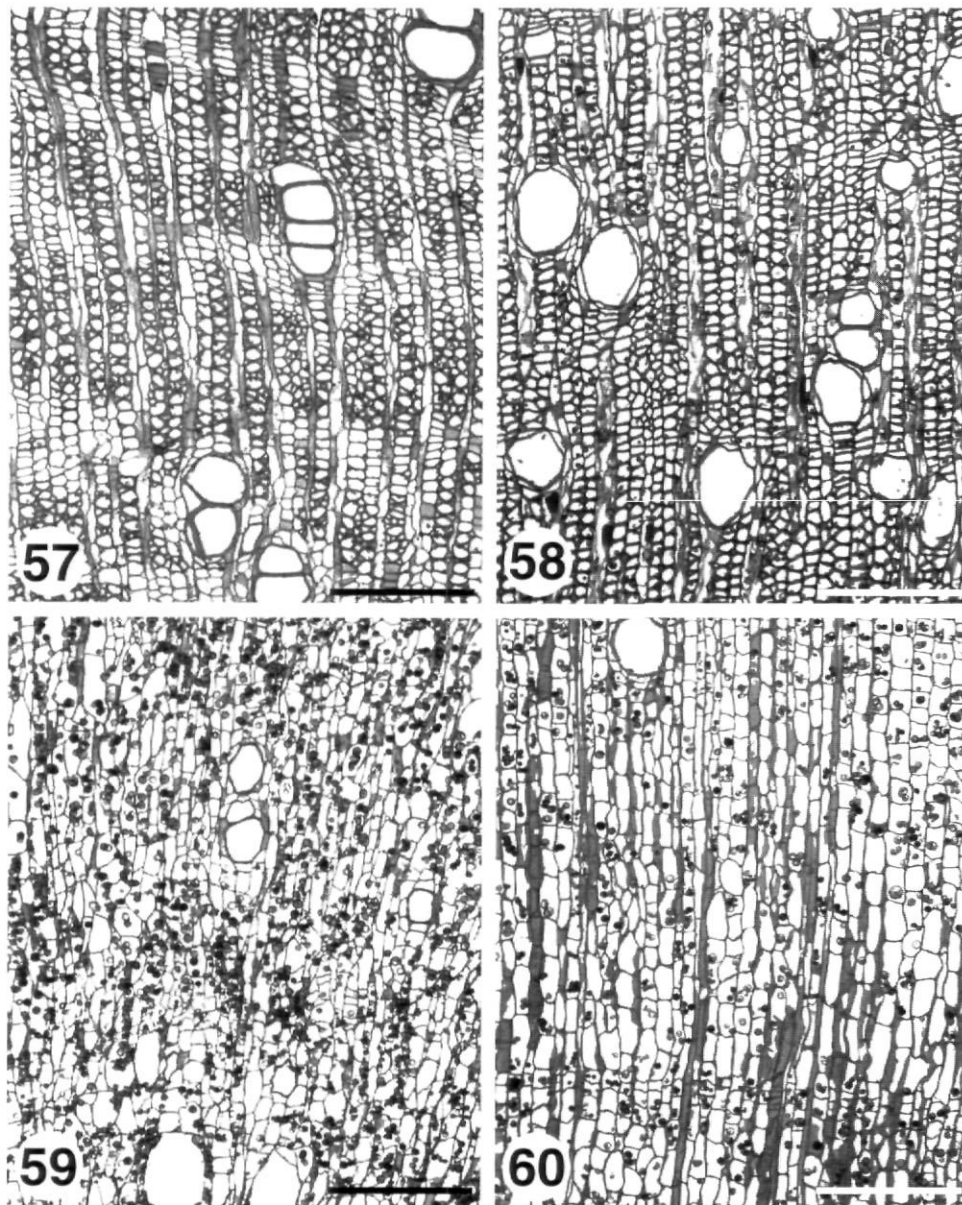
Figures 53–56. Root XSs of bottle trees and sarcorhizal trees showing structural plan consisting of wide bands of PP alternating with occasional bands of LFs. Scale bars = 500 μm . Fig. 53. *M. drouhardii* Olson 679. Fig. 54. *M. stenopetala* Olson 675. Fig. 55. *M. arborea* Olson 714. Fig. 56. *M. ruspoliana* Olson 702.

der trees and bottle trees. The sarcorhizal trees have multiseriate rays of intermediate height, and the tuberous shrubs have by far the tallest rays. The rays of bottle trees were composed of 88.25% procumbent cells, and those of the slender trees 84.67%. Percentages are much lower in the rays of sarcorhizal trees (56.5%) and tuberous shrubs (39.4%). Similar percentages of square cells were observed in both sarcorhizal trees and tuberous shrubs. The highest proportion of upright cells was observed in the tuberous shrubs. Uniseriate rays are markedly taller in the tuberous shrubs than in the other life forms. Short

uniseriate wings on multiseriate rays were observed in most species. However, two bottle trees (*M. ovalifolia* and *M. stenopetala*) and two slender trees (*M. cananensis* and *M. oleifera*) are distinguished by apparently lacking these wings.

Idioblasts and secretory tissues

Moringa wood and bark contains druses and rhomboidal crystals, cells with strongly-staining contents presumed to be gum cells, and cells with very dark brownish or greyish contents. There is great variation



Figures 57–60. Root XSs of slender trees and tuberous shrubs. Scale bars = 500 μ m. Fig. 57. *M. concanensis* Olson 700, showing an area of the root where bands of PP are common in addition to bands of LFs. Fig. 58. *M. peregrina* Olson 567, showing an area in which AP is confined to a single layer of VP around vessels. Fig. 59. *M. borziana* Olson 707 and Fig. 60. *M. rivae* Olson 701 illustrate the absence of libriform fibres and the great abundance of parenchyma in the tuber secondary xylem. Starch is abundant in the cells of all tuberous species.

in the distribution of these cell contents, but it is manifested at an interspecific level and does not strongly correspond to differences between life form classes. For example, rhomboidal crystals and druses are found in all *Moringa* species, but each species exhibits a different combination of cell types in which rhomboidal crystals or druses are found (Figs 98–105, 110; Appendix 3). Likewise, tyloses were observed in all species (e.g. Figs 92, 93), as were lysigenous gum canals in the pith (Fig. 95), gum cells in rays and

bark (Fig. 96), and cells with brown or dark-staining contents in various parts of the bark (Figs 97, 110).

Gum ducts are occasionally seen in the bark and appear always to be associated with traumatic events (Figs 108, 109; see also Subrahmanyam & Shah, 1988).

Storying

Storying can be observed in all *Moringa* species but is most apparent in areas of extensive axial parenchyma

Table 1. Stem and root structural plans

Life form	Stem plan + LF shapes	Root plan
Bottle trees + <i>M. arborea</i>	Confluent bands of paratracheal axial parenchyma alternating with bands of libriform fibres	Similar to stem
<i>M. ruspoliana</i> (sarcorrhizal tree)	Alternating bands of short, wide parenchyma-like libriform fibres and long, narrow libriform fibres	Similar to bottle trees
Slender trees	Fibres of varying shapes and sizes, but not partitioned into bands; aliform axial parenchyma may be present	Alternating bands of libriform fibres and axial parenchyma; parenchyma bands not wider than bands of fibres, sometimes rare
Tuberous shrubs	Narrow libriform fibres sometimes varying in size with season; sometimes with bands of paratracheal axial parenchyma	Secondary xylem almost entirely axial parenchyma, with no libriform fibres (or extremely rare)

or short libriform fibres. Thus, storying of rays, vessels, and axial parenchyma cells is usually conspicuous in bottle trees and *M. arborea* (e.g. tangential sections of Figs 4–20). Even when some elongation of fibres occurs, rays or vessels often are storied (e.g. tangential sections of slender trees in Figs 28–36, and tuberous shrubs in 48 and 52).

Bark

The ephemeral-stemmed species differ from the arboreal species in the configuration of phloem fibres at maturity. Bark in young stems of all species have distinct wedges of phloem fibres that are not crushed at maturity (Fig. 106). In the larger stems of the three arboreal life forms, the phloem fibres being produced are mostly thin-walled and crushed at maturity (Fig. 108). *Moringa rivae*, the largest tuberous shrub and the only one of that life form to produce permanent stems, sometimes shows this bark type. The remainder of the tuberous shrubs have bark with wedges of intact phloem fibres (Fig. 107).

Variation at the interspecific level in the occurrence of sclereids in phelloderm, cortical parenchyma, and phloem rays is conspicuous (Fig. 110).

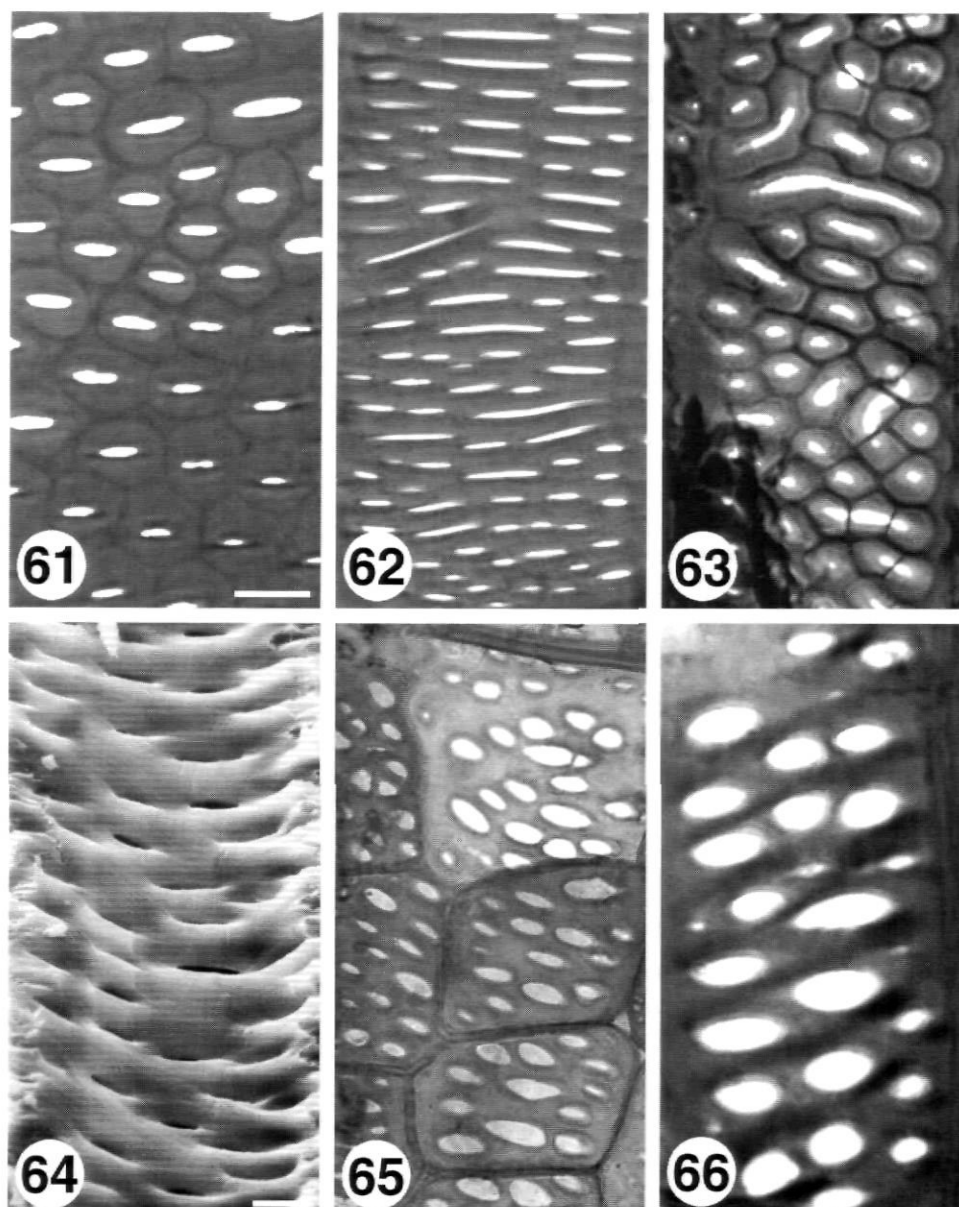
SEASONAL AND INTERPOPULATIONAL ECOLOGICAL VARIATION

There is much to be investigated regarding the ecological correlations of variation in wood. Wood responds to small differences in environmental conditions, and fine sampling at the population level is ideal for revealing these patterns. Although sampling in the current study is on a very broad scale, species of which samples were collected from areas of differing moisture availability show consistent patterns of variation in

quantitative and qualitative characters (e.g. wider vessels are associated with moister conditions).

Ecological trends in the Moringaceae are most usefully considered within the context of their unusual combination of features that characterize succulents combined with others that are more typical of mesic woody plants. For example, the bottle tree *Moringa* species greatly exceed the mean value of vessel diameter in a sample of stem succulents drawn from dicotyledons at large and in this respect resemble mesic woody plants (147.84 µm bottle trees vs 72 µm stem succulents; Carlquist, 1975: 206). However, the conductive area of *Moringa* bottle trees (0.12 mm² mm⁻²) approaches that of the stem succulents (0.87 mm² mm⁻²). The enormous quantity of water storage tissue, in combination with the propensity to drop their leaves at the first sign on drought, seem likely to allow *Moringa* bottle trees to lead a dual lifestyle. Leaf loss, in combination with large amounts of water storage tissue suggest that the bottle trees can persist through dry periods while preventing highly negative xylem pressure potentials. Thus, when leafless, bottle trees resemble stem succulents. When water is available, very wide vessels should provide efficient conduction comparable to the vessels of a mesic tree. The dual lifestyle comes with a compromise in the form of lower conductive area per square mm of wood in bottle trees as compared to more mesic trees. A consequence is that the proportion of leaf area to stem volume in *Moringa* bottle trees is likely less than in mesic trees.

In contrast, a sample of shrubs from drylands shows a strong tendency to have high densities of very narrow vessel elements (Carlquist, 1975: 206). Though not directly comparable in habit, tuberous shrub *Moringa* species show a similar tendency toward conductive

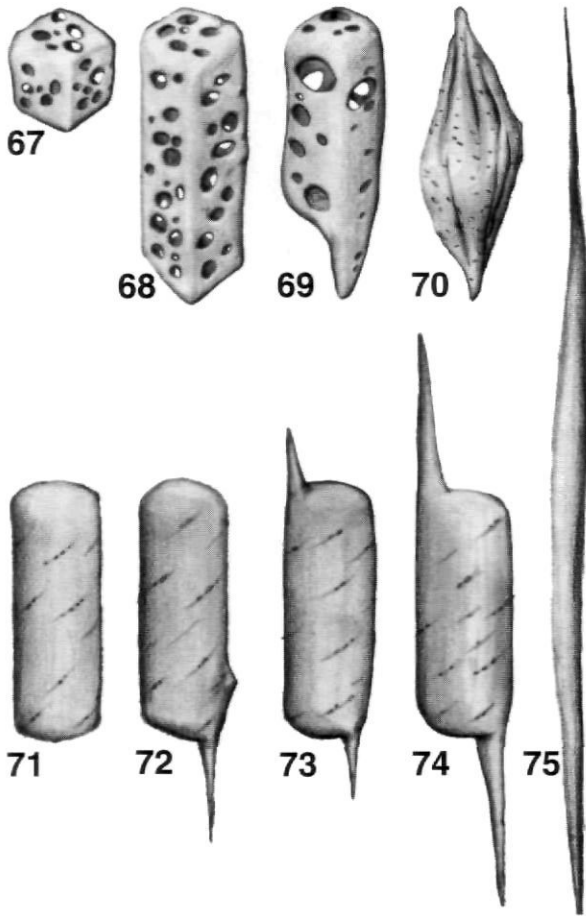


Figures 61–66. Vessel wall pitting. Scale of Figures 61–63 and 65 and 66 shown in Fig. 61; scale bar = 100 μm ; scale bar in 64 = 10 μm . Fig. 61. *M. concanensis* Olson 700 V-V pitting typical of such pitting throughout the genus, showing the narrowly oval apertures and polygonal pit cavities. Fig. 62. *M. arborea* Olson 714 V-V pitting occasionally narrowly oval to gash-like. Fig. 63. *M. borziana* Olson 678 V-V pitting occasionally highly irregular with apertures of some adjacent pits confluent. Fig. 64. *M. rivae* Olson 677 SEM of interior of Ve showing pit apertures arranged in shallow helical grooves, especially apparent toward bottom of micrograph. Fig. 65. *M. ruspoliana* Olson 703 V-AP pitting showing irregularly alternate arrangement of pits, oval apertures with narrow borders, and aggregation of pits on V wall into fields corresponding to the faces of contacting P cells. Fig. 66. *M. longituba* Olson 704 V-AP pitting showing arrangement of pits in shallow helical grooves.

safety through a much greater number of smaller, more conductively safe, vessels per unit area than the arboreal species. Tuberosous shrubs have shallower roots and much smaller water storage organs than the arboreal species, and would therefore seem likely to be more vulnerable to desiccation than the larger species.

Seasonal within-plant variation

Seasonal variation in the characteristics of growth rings represents very fine-scale ecological variation that allows woody plants to optimize their use of available moisture. It is assumed that both wider growth rings and the cells that make them up are



Figures 67–75. Axial parenchyma and libriform fibre diversity in *Moringa*. Figures 67–70. P cells. Fig. 67. Typical cuboidal P cell with large pits. Fig. 68. Axially elongate but still angular P cell with distinct pits. Fig. 69. As the result of packing with neighboring cells, some P cells have small irregular 'tails'. Fig. 70. Large, sparsely-pitted P cells can collapse to a wide fusiform shape in macerations, particularly common in *M. hildebrandtii*. P cells are often part of strands, in contrast to LFs. Figures 71–75. LFs. Fig. 71. P-like LF lacking the tails resulting from intrusive elongation. Fig. 72. Asymmetrically elongated P-like LF with only one tail. Fig. 73. Wide, P-like LF with very short tails. Fig. 74. Wide LF with distinct tails. Fig. 75. Typical slender LF greatly elongated by intrusive growth.

indicative of greater available moisture than narrow rings and cells, but this assumption was not tested in this study.

In the bottle trees and *M. arborea*, moister conditions lead to the production of wider parenchyma cells in the bands of confluent paratracheal parenchyma that characterize the earlywood of these species. Toward the end of the season, a band of libriform fibres is

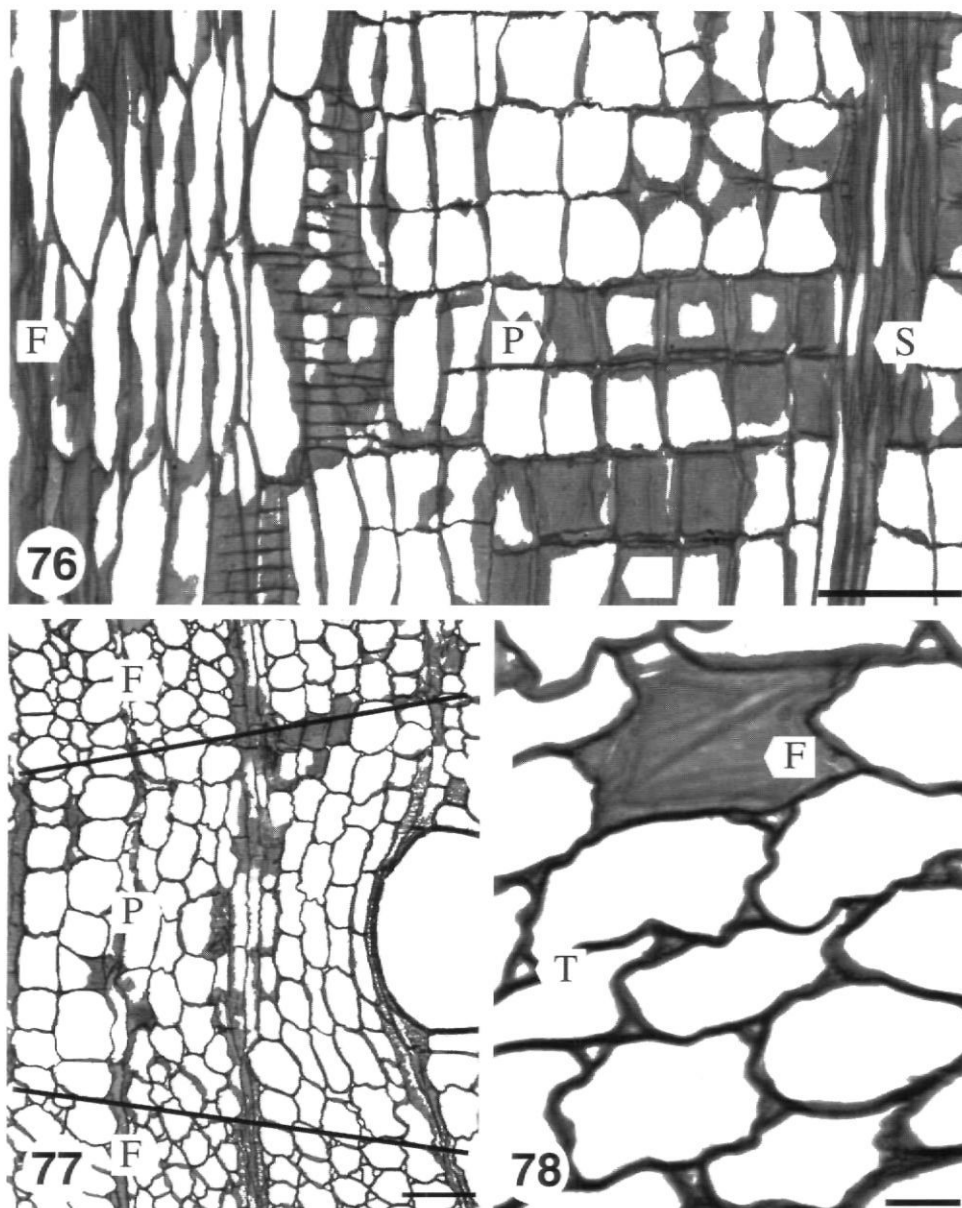
usually produced. These cells also tend to be larger with moister conditions (e.g. Fig. 76). However, in *M. ovalifolia*, the bottle tree that occupies the driest habitat of the four species in this habit class, very dry growth seasons are frequent and lead to the production of only very small parenchyma cells and no libriform fibres (Fig. 10). This phenomenon may occur in the other bottle trees given sufficiently dry conditions, but no such samples were found.

In *M. concanensis*, *M. borziana*, and *M. rivae*, and very rarely in *M. peregrina*, production of an earlywood parenchyma band is facultatively dependent on a sufficient amount of moisture. Otherwise, libriform fibres are produced that may show slight decrease in diameter with a decrease in moisture across the growing season (e.g. Figs 26, 50). Such a pattern is also seen in the tuberous shrubs *M. longituba* and *M. pygmaea*. The extreme of this pattern is seen in *M. ruspoliana*, which produces very wide, parenchyma-like libriform fibres early in the season and grades to long, thin ones before ceasing growth for the season. Despite marked wet and dry seasons in habitat, variation in libriform fibre diameter correlated with seasonal flux in moisture availability is difficult to detect in *M. oleifera* and *M. peregrina*, and uncommon in *M. concanensis*, suggesting very rigid developmental control of fibre production.

Interpopulational intraspecific variation

Differences can also be detected between collection localities of the same species that differ in moisture availability. The different localities where a given species was collected were ranked according to estimated relative moisture availability based on soil, slope, and type and extent of vegetation cover (summarized in Appendix 1). Vessel elements track moisture availability closely, tending to be longer and wider in moister localities. Vessel density and conductive area also tend to be higher with increasing moisture. These observations hold true particularly for the arboreal *Moringa* species, which have permanent shoots. While the stems of arboreal species persist through severe droughts, those of tuberous shrubs are shed. These ephemeral shoots reflect only the few seasons in which they have persisted, which may or may not mirror the long-term moisture availability of a site.

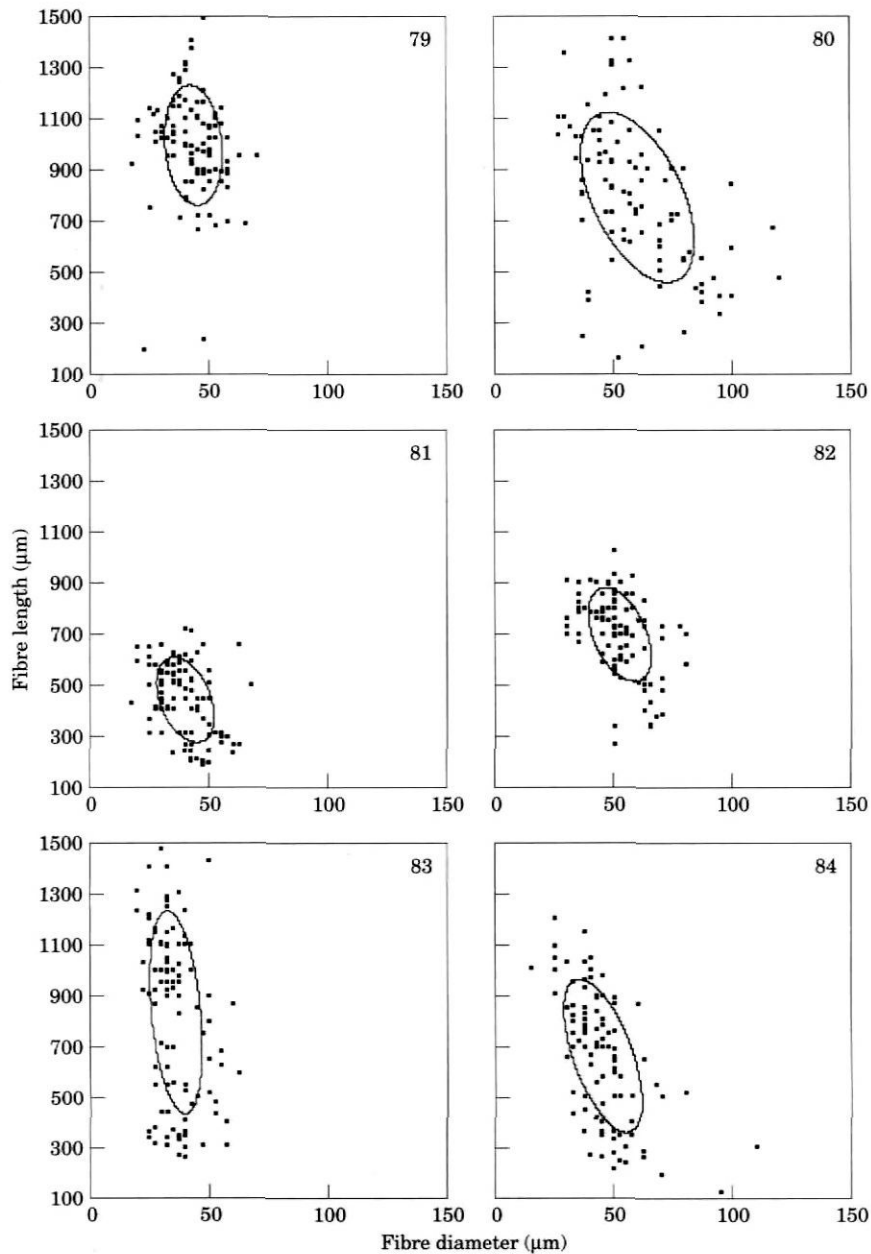
In the bottle tree *M. drouhardii*, vessel element length was 238.1 μm in the driest locality visited (Olson 695). A longer mean vessel element length of 293.20 μm was recorded from the most mesic locality visited (Olson 679). Vessel diameter also appears to track moisture availability closely, ranging from 129.2 μm in the driest locality (Olson 695) to 203.4 μm in the moistest (Olson 679). Vessels per group ranged from 1.4 in the driest locality (Olson 695) to 2.2 in



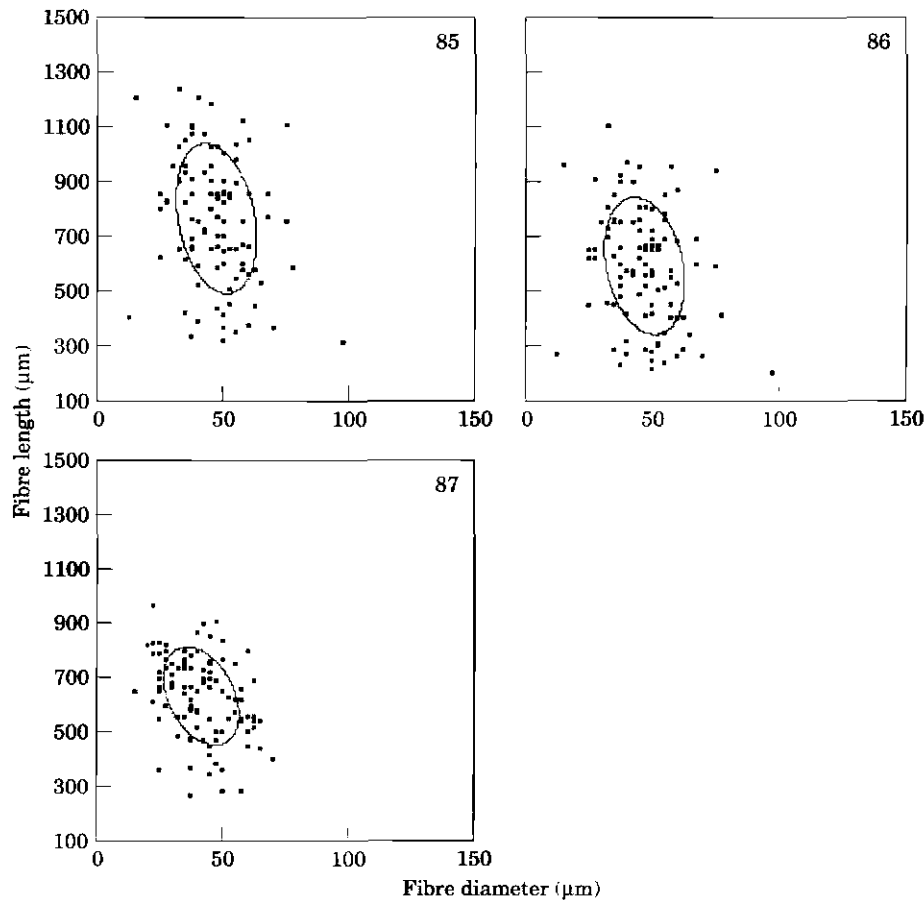
Figures 76–78. Parenchyma and libriform fibre diversity in *Moringa*, continued. Scale bar in 76 = 500 μm , in 77 and 78 = 100 μm . Fig. 76. *M. hildebrandtii* Olson 693 radial view showing very wide LFs on L ('F'), corresponding to LF types in Figures 71–73. Large, cuboidal P cells span the inner part of the figure ('P'). These cells resemble cell types in Figures 67 and 68, and in macerations resemble the cell in Fig. 70. Long, slender LFs corresponding to the type in Fig. 75 are in a narrow band ('S'). Figures 77 and 78. *M. drouhardii* Olson 679. Fig. 77. Similarity of LFs and P cells in XS. An earlywood band of P that includes the V in this image is labelled 'P' between black lines. These cells tend to be more angular in section than LFs, with intercellular spaces small or absent and no intrusive tails between cells. In contrast, the LFs in the areas labelled 'F' are more rounded in section, with intercellular spaces and intrusive tails common. Fig. 78. Closer view of LFs to show very broad perpendicular end wall of LF at top of figure ('F'). The small space where the end wall has been sectioned away represents the removal of the short tail. Such a tail in section is indicated by 'T'. These LFs correspond to the types depicted in Figures 72 and 73.

the most mesic (Olson 679). Vessel density was quite variable, with counts at the driest locality (Olson 695) ranging from 2.91 vessels mm^{-2} to 5.75 vessels mm^{-2} from different areas of the highly contorted

trunk of the same tree at the same distance from the ground. This last count is close to the highest density found in the species of 5.89 vessels mm^{-2} , observed at the most mesic locality (Olson 679),



Figures 79–84. Scatterplots of dimensions of 100 LFs from stems of bottle trees and sarcorhizal trees. Ellipse encircles 50% of data points. Figures 79–82. Bottle trees. Fig. 79. *M. drouhardii* Olson 679. Points in the upper L of the scatterplots represent long, slender LFs such as the one in Fig. 75. *M. drouhardii* relies on AP for storage and has few short, wide, parenchyma-like fibres (points in the lower right of the scatterplots). Figures 80–82 show ellipses strongly inclined from the upper L (long, slender LFs) to the lower R (short, wide LFs) and suggest a greater diversity of function for LFs in these species, with long, narrow LFs serving chiefly as support, and very wide LFs converging on a parenchymalike function. *M. ovalifolia* scatterplot in Fig. 81 similar to those of the other bottle trees, but with a smaller mean cell size and variance likely associated with the more arid conditions in its habitat than in those of the other bottle trees. Figures 83 and 84. Sarcorhizal trees. Fig. 83. *M. arborea* Olson 714 showing scarcely inclined ellipse as in Fig. 79, but with a much greater span of fibre length. As in *M. drouhardii*, LFs in *M. arborea* serve mostly a support function, with PP functioning in storage. Fig. 84. *M. ruspoliana* Olson 703. In contrast to *M. arborea*, *M. ruspoliana* lacks PP. Long, slender LFs also serve a support function in this species, but instead of AP, abundant short, wide LFs serve as the axial storage tissue in this species. This diversity of LF form is reflected in the inclined ellipse from upper L toward the lower R. The two species that rely on libriform fibres chiefly for support, *M. drouhardii* and *M. arborea*, show similar patterns.



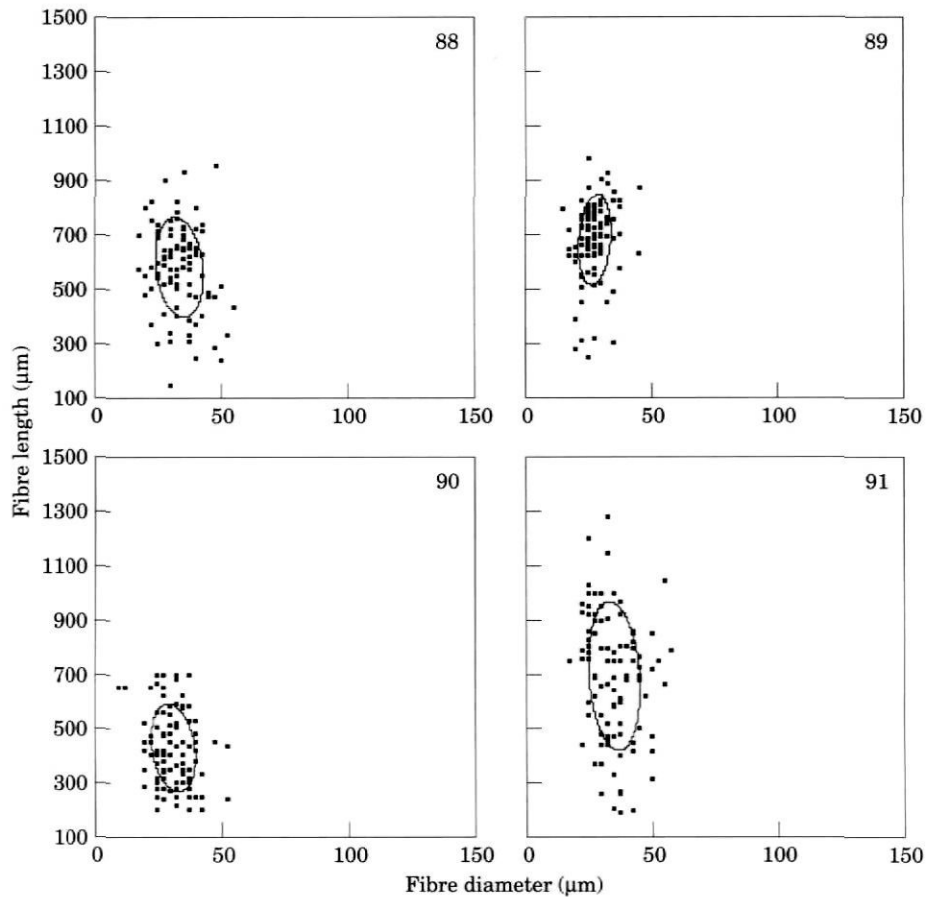
Figures 85–87. Scatterplots of dimensions of 100 LFs from stems of slender trees. Ellipse encircles 50% of data points. In XS and RS, LF shape in slender trees does not appear to be partitioned into markedly different bands as in some species, e.g. *M. ruspoliana*. Broad clouds and wide ellipses with a slight angle in these scatterplots illustrate that nonetheless there is diversity in LF shape in these species. These different libriform fibre shapes are distributed uniformly throughout the stem. Fig. 85. *M. concanensis* Olson 700. The only slender tree to produce appreciable amounts of PP, the ellipse in this plot may show a slightly more vertical tendency than those in the plots of the other slender trees (i.e. less tendency to produce short, wide LFs). Fig. 86. *M. oleifera* Olson s.n. also shows a broad distribution of LF shape. Fig. 87. *M. peregrina* Olson 567. Scatterplot similar to those of the other slender trees, but with a smaller variance. *M. peregrina* occupies the most arid habitat of the slender trees. A similar compression of the scatterplot is seen for *M. ovalifolia*, which occupies the most arid habitat of the bottle trees.

while the cultivated tree (Olson 696) had 4.06 vessels mm^{-2} . Conductive area varied from a low of 0.08 $\text{mm}^2 \text{mm}^{-2}$ (Olson 695) to 0.14 $\text{mm}^2 \text{mm}^{-2}$ at the most mesic locality (Olson 679).

A similar pattern of interpopulation variation was observed in the tuberous shrub *M. rivae*. Olson 677, collected from the rocky slope of a granitic dome in the Kaisut Desert region of central Kenya, had a vessel diameter 81.10 μm and a conductive area of 0.07 $\text{mm}^2 \text{mm}^{-2}$. *M. rivae* Olson 701, from a moister locality on the deep soil of the Dawa River floodplain in north-eastern Kenya, had wider vessels (141.60 μm) and a higher conductive area of 0.12 $\text{mm}^2 \text{mm}^{-2}$. However, vessel density was much higher at the dry locality

than at the moister one, meaning that Olson 677 sacrifices some conductive efficiency for safety in its dry habitat by producing many narrow vessels. On the other hand, Olson 701 with more dependable moisture sacrifices some safety for more rapid conduction with fewer, much larger vessels.

In contrast, vessel measurements from the species of tuberous shrubs with ephemeral shoots do not always clearly correlate with estimated moisture availability. Ephemeral stems, however, can only reflect the few seasons of growth that they have experienced, and the highly irregular rainfall of the Horn of Africa often shows great annual deviations from long-term trends. For example, *M. borziana* Olson 678 was collected in



Figures 88–91. Scatterplots of dimensions of 100 LFs from stems of tuberous shrubs. Ellipse encircles 50% of data points. *M. borziana* (Fig. 88) and *M. rivae* (Fig. 91) have fascicular storage in the form of occasional bands of paratracheal AP. These species also show a greater diversity of LFs than the other species of tuberous shrubs. In contrast, storage in *M. longituba* (Fig. 89) and *M. pygmaea* (Fig. 90) is performed predominantly by the tuber, and the slender LFs serve chiefly in support.

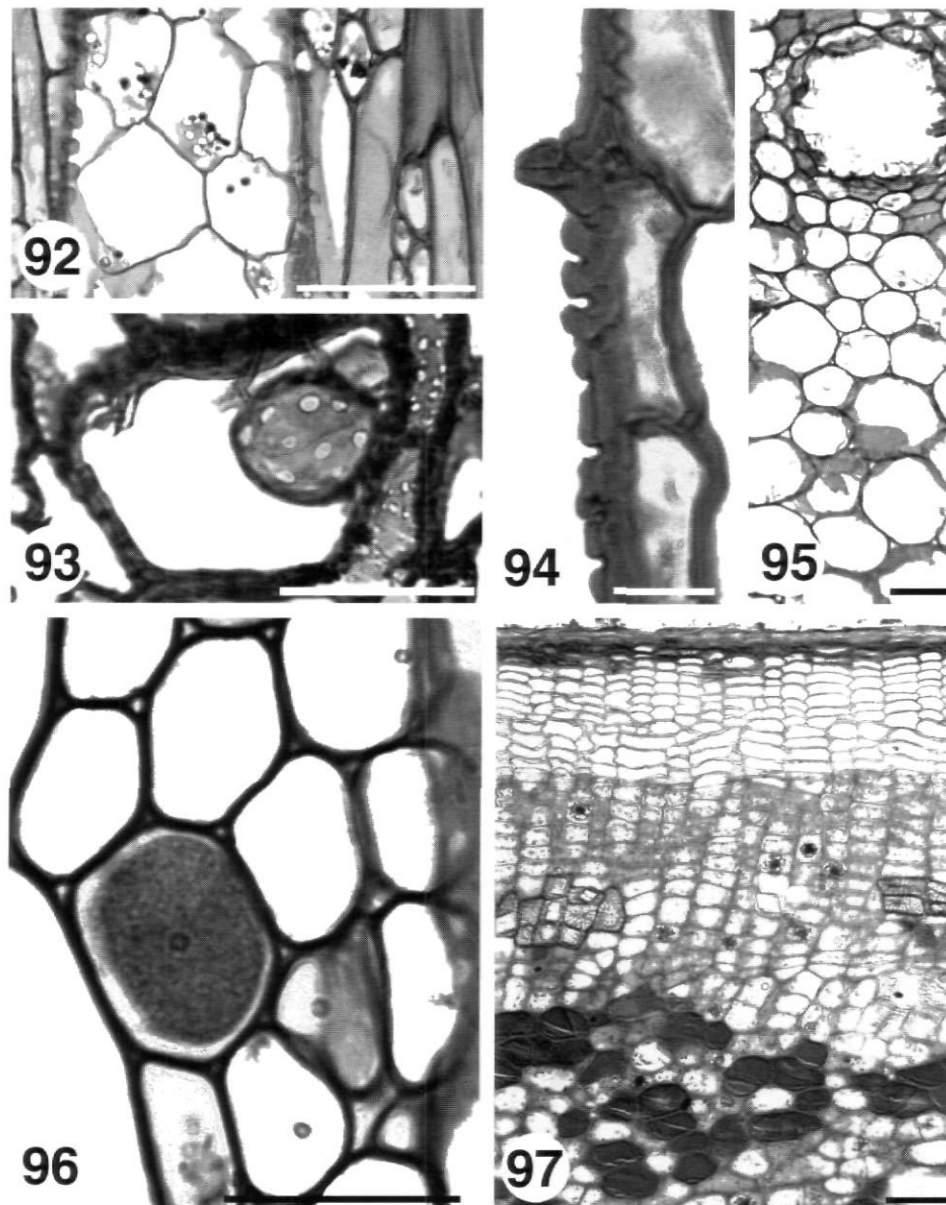
dry scrub as opposed to the apparently moister habitat of Olson 707 that supported low tropical deciduous forest. Vessel diameter is consistent with this assessment, being smaller (60.50 μm) in Olson 678 and wider in Olson 707 (95.20 μm). However, Olson 678 had more vessels per unit area and a higher conductive area (0.20 $\text{mm}^2 \text{mm}^{-2}$) than Olson 707 (0.14 $\text{mm}^2 \text{mm}^{-2}$) from the moister habitat. Likewise, *M. longituba* Olson 704 was collected from a low hill on the fringe of the Dawa floodplain in very rocky soil in open deciduous scrubby thorn forest. The habitat of Olson 708 and 712 appeared to be moister, supporting denser cover in a mosaic of taller tropical deciduous forest and grassland. Despite apparent long-term differences in moisture availability at these sites, the conductive area of all these collections of *M. longituba* were very similar.

PHYLOGENETIC UTILITY OF WOOD ANATOMICAL CHARACTERS

Wood anatomical information in *Moringa* suggests relationships based on overall similarity, and provides characters of potential utility in phylogeny reconstruction based on shared derived characters. The congruence of wood anatomical characters with other anatomical, morphological and molecular characters in a phylogenetic context is the subject of current investigation, but some comments relating exclusively to wood anatomy are summarized here.

Characters of potential phylogenetic utility at the interfamilial level

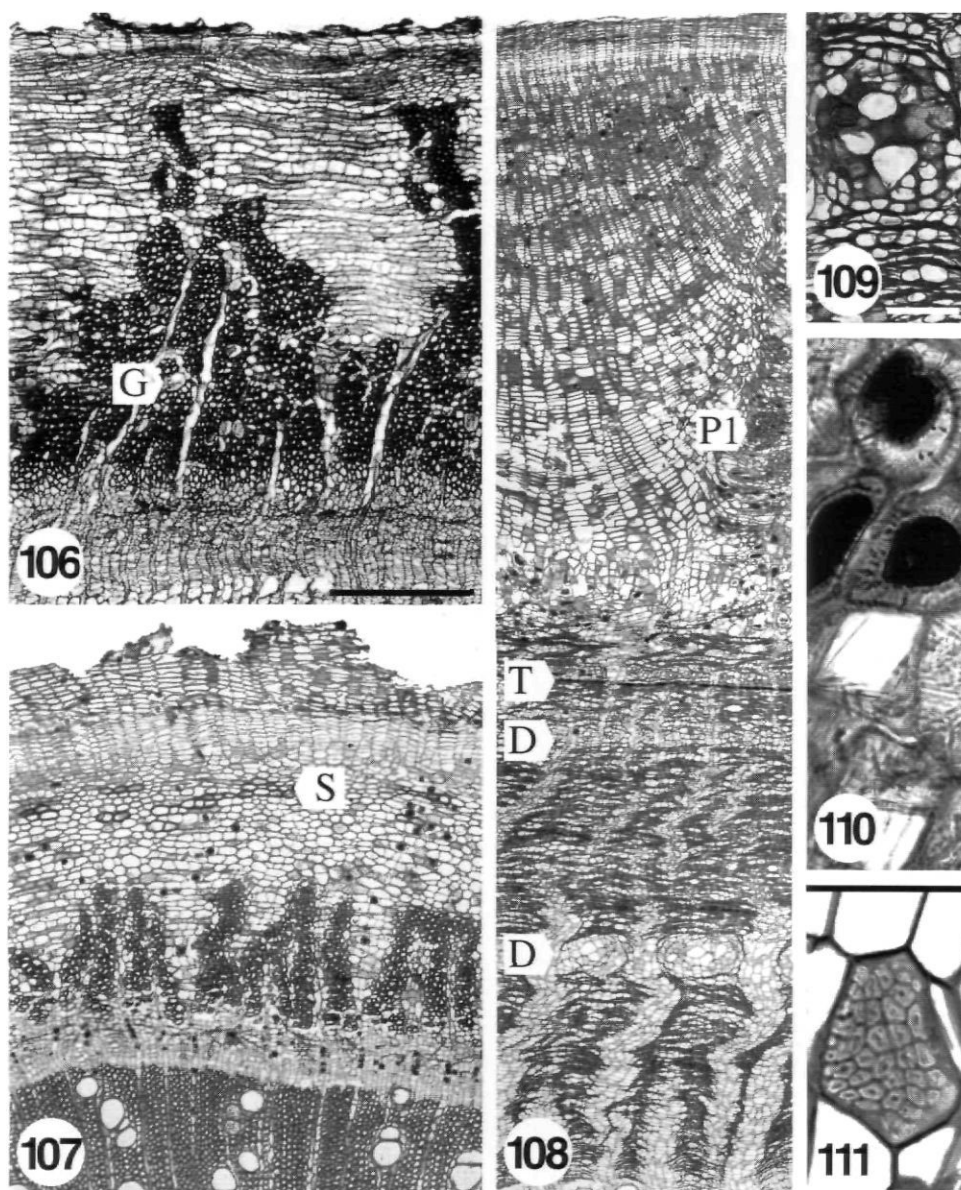
It is of great interest to evaluate interpretation of characters including wood in the context of the phylo-



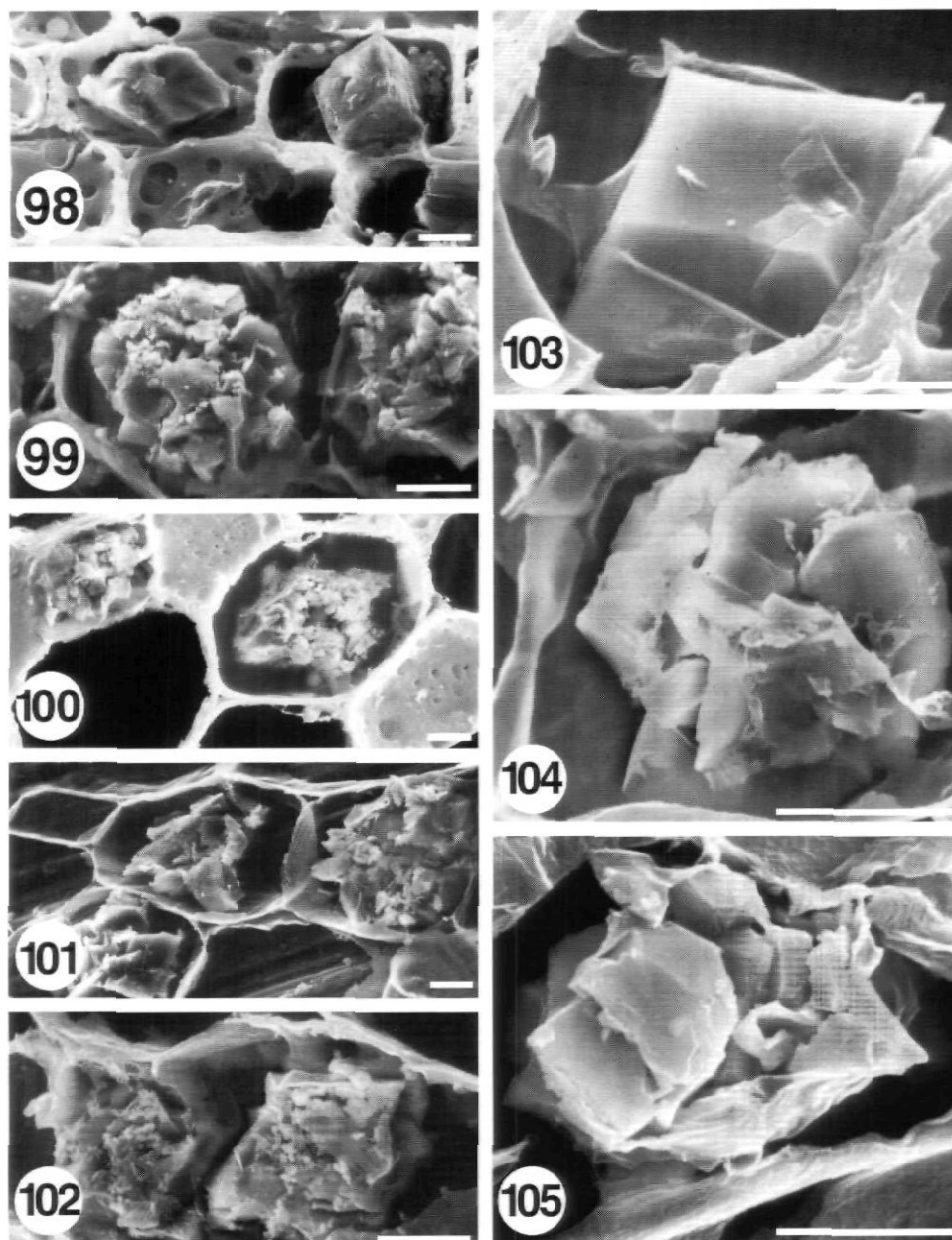
Figures 92–97. Vessel features, pith gum duct, idioblasts. Scale bar in 92, 93, 97 = 100 μm , in 94 = 15 μm , in 95 = 500 μm , in 96 = 50 μm . Fig. 92. *M. ruspoliana* Olson 702, starch-containing tyloses in TgS. Fig. 93. *M. hildebrandtii* Olson 697 conspicuously-pitted tylosis in XS. Pits on end walls of VP cells to R of V. Fig. 94. *M. hildebrandtii* Olson 693 V wall in RS showing sculpting of interior of V wall and non-bordered perforation plate; VP to R of V. Fig. 95. Pith of *Moringa* species usually contains 1–3 axially oriented lysigenous gum ducts (*M. stenopetala* Olson 675 shown). Fig. 96. TgS *M. arborea* Olson 714 gum cell in ray; gum cells are differentiated from other cells by contents, but not by shape or pitting. Fig. 97. XS *M. hildebrandtii* Olson 697 bark showing cells with brown contents at bottom of image, scattered druses and rhomboidal crystals, rhomboidal crystal-containing sclereids in cortical P.

genetic framework provided by molecular phylogenetic studies. This is especially true in the case of the Moringaceae and Caricaceae because a sister family relationship between the two families was not suspected before these studies. In fact, there is a strong resemblance between the wood of *Carica* and the only African member of the Caricaceae, *Cylicomorpha*, and

the bottle tree *Moringa* species. Based on wood anatomy and geography, the most likely sister genus to *Moringa* is *Cylicomorpha*. Carlquist (1998) found strong similarity between the woods of *Carica* and *Cylicomorpha* and the bottle tree *M. hildebrandtii*. Among the similarities noted between these taxa were ray structure, cortical druses, lignified paratracheal



Figures 106–111. *Moringa* bark. Scale for Figures 106–108 shown in 106; scale bar = 500 µm, in 109 and 110 = 100 µm, in 111 = 50 µm. Fig. 106. Bark of young stem of bottle tree *M. stenopetala* Olson 675, with phloem fibres arranged in wedges separated by dilated phloem rays. Gum cells are scattered in the phloem fibre wedges, one indicated by a 'G'. Active phloem at bottom of image. Fig. 107. *M. longituba* Olson 712 bark, representative of bark of tuberous shrubs. The bark of mature stems of the tuberous shrubs is more similar to that of the juvenile arboreal species (Fig. 106) than to that of the adult arboreal species (as in Fig. 108), with wedges of phloem fibres separated by dilated phloem rays. Scattered fields of thin-walled sclereids in outer cortical P, one of which is indicated by an 'S'. Irregular fissuring of phellem at top. Fig. 108. *M. drouhardii* Olson 679 with bark typical of the arboreal *Moringa* spp. with often crushed thin-walled phloem fibres in elongate ranks at bottom half of image. Occasional patches of intact thicker-walled phloem fibres persist from the wedges in young wood. One such patch is indicated by 'P1'. 'D's indicate gum ducts arranged in occasional rings within the wedges of phloem fibres and are likely associated with traumas. The lower ducts are functional, whereas the upper ones are mostly crushed. 'T' indicates a row of cells containing brown bodies. Druses and sclereids are abundant in the extensive cortical P and phelloderm. Fig. 109. Traumatic gum duct in bark of *M. ovalifolia* Olson 718 showing enlarged intercellular spaces. Fig. 110. Sclereids with dark contents and rhomboidal crystals in the outer cortical P of *M. concanensis* Olson 700. Fig. 111. *M. oleifera* Olson s.n. reticulate pattern of sieve plate pores.



Figures 98–105. Crystals in wood, bark, and pith of *Moringa*. Scale bars = 10 μm . Fig. 98. *M. arborea* Olson 714 rhomboidal crystals in xylem ray, starch grain at upper L. Fig. 99. *M. peregrina* Olson 567 druses in pith. Fig. 100. *M. arborea* Olson 714 rhomboidal crystals in pith (crystals show damage from sectioning). Fig. 101. *M. longituba* Olson 712 druses in outer cortical P. Fig. 102. *M. concanensis* Olson 700 rhomboidal crystals in phelloderm serving as nuclei for the formation of further crystals and thus transitional to druses. Such crystals are much rarer than either rhomboidal crystals or druses. Fig. 103. *M. rivae* Olson 677 rhomboidal crystal in phloem ray showing enclosing membrane. Fig. 104. *M. arborea* Olson 714 druse in phloem ray. Fig. 105. *M. rivae* Olson 677 rhomboidal crystal transitional to druse in phloem ray.

parenchyma, and storing. The present study has noted the similarity of *Carica* and *Cylicomorpha* not only to *M. hildebrandtii* but to the other bottle trees as well. *Moringa drouhardii* appears to be most similar to the Caricaceae because of all the bottle trees libri-

form fibres play the most restricted role in this species. This anatomical similarity seems likely to be reflective of phylogenetic relationship rather than entirely due to habit and ecology, because, while there are numerous dry tropical representatives in the caricaceous genera

Jacaratia, *Jarilla*, and some *Carica*, *Cylicomorpha* is restricted to wet montane tropical forest (Badillo, 1971).

The chief difference identified between the families by Carlquist (1998) was the absence of articulated laticifers in *Moringa*. These structures were not observed in any species of *Moringa* in the present study. Secretory ducts in *Moringa* are intercellular, as opposed to the articulated latex-conducting cells in the Caricaceae. In the absence of trauma, canals in *Moringa* are produced only in the pith, and never found in tangential plates in the secondary xylem or as normal features of the bark as are laticifers in many Caricaceae. The yellow to reddish gum often oozing from *Moringa* gum ducts appears to bear little superficial similarity to the milky latex of Caricaceae. Thus the system of ducts in *Moringa* bears little resemblance to that in the Caricaceae in location, structure, or function and it seems best to regard them as non-homologous features. On the other hand, hollowings in the pith appear to be at least occasional features in Caricaceae. The central parts of *Cylicomorpha* trunks are reported to become hollow with age (Badillo, 1971) and these may be homologous to the pith hollowings of *Moringa*.

Characters of potential phylogenetic utility at the interspecific level

At a coarse level, wood anatomy suggests that *Moringa* is divided into three groups: bottle trees, slender trees, and the sarcorrhizal trees plus tuberous shrubs. For example, the strong similarity of structural plan within the bottle trees suggests that they may be closely related. The same is true for the slender trees. Lack of strong anatomical coherence between the sarcorrhizal trees suggests that similarity of life form may be superficial and not indicative of relationship. However, similarity in vessel and fibre dimensions despite strong differences in habit and ecology between the sarcorrhizal trees and tuberous shrubs seems likely to be indicative of relationship between these groups.

At a finer level, wood anatomy may provide characters that can help diagnose relationship within the broad groups outlined above. For example, absence of both callose plugs in living phloem and uniseriate wings on multiseriate rays probably reflects close relationship between *M. oleifera* and *M. concanensis*. The sarcorrhizal tree *M. ruspoliana* lacks bands of paratracheal axial parenchyma in the secondary xylem and therefore may be more closely related to *M. longituba*, a tuberous shrub that also has this trait (the scant samples of *M. pygmaea* available also lack paratracheal axial parenchyma). Presence or absence of crystals in different cell types also represents a potential source of characters (summarized in Appendix

3). For example, the presence of crystalliferous tyloses only in *M. arborea* and *M. rivaie* suggests a close relationship between these species, the former a sarcorrhizal tree and the latter the largest of the tuberous shrubs. Intraspecific variation in the distribution of crystals was noted between the type locality of *M. longituba* (Olson 704) and the southernmost localities (Olson 708 and 712), potentially providing additional understanding of this widespread and variable species.

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APPENDIX 1

COLLECTION LOCALITIES AND VOUCHER INFORMATION

Species	Collector and #	Locality	Habitat (when more than one collection has been made per sp., listed from dry to moist)	Latitude and longitude	Herbaria with vouchers
<i>M. arborea</i>	Olson 714	Kenya: Northeastern Province: Mandera District: c. 35 km NW of Rhamu on road to Malka Mari, in small rocky canyon called Garse	Near bottom of limestone lugga (dry watercourse)	4°03'08"N 41°00'02"E	MO, EA, FT, K
<i>M. borziana</i>	Olson 678	Kenya: Coast Province: Taita District: SW Tsavo East National Park Voi gate	Disturbed grassland/shrubland mosaic	3°21'49"S 38°35'34"E	MO, EA, FT, K
	Olson 707	Kenya: Coast Province: Kilifi District: Galana River Camp	Disturbed dense, low tropical deciduous forest	c. 3°06'S 39°24'E	MO, EA, FT, K
<i>M. concanensis</i>	Olson 700	India: Tamil Nadu: Udumalpet Dist. Combatore Rd. to Parapaddur Dam in Palni Hills c. 200 km WSW of Tiruchirapalli	Steep slope in dense tropical deciduous forest	10°28'31"N 77°44'57"E	MO, EA, FT, K
<i>M. drouhardii</i>	Olson 695	Madagascar: Tulear, above Grotte de Sarodrano, south of Tulear	In scrub on exposed rocky limestone slope near ocean	23°31'00"S 43°45'12"E	MO, EA, FT, K, TAN
	Olson 694	Madagascar: Tulear: Along Onilahy River near Ambohimahavelona, SE of Tulear	Densely vegetated slopes of steep limestone canyon	23°27'06"S 43°55'51"E	MO, EA, FT, K, TAN
	Olson 679	Madagascar: Tulear: near Amboasary	Dense deciduous forest on deep soil; moistest wild locality	25°00'S 46°25'E	MO, EA, FT, K, TAN
	Olson 696	Madagascar: Tulear: cultivated in watered garden	Well-watered garden	23°20'S 43°40'E	MO, EA, FT, K, TAN
<i>M. hildebrandtii</i>	Olson 693	Madagascar: Tulear: cultivated in village of Vorehe	Windbreak, apparently unwatered	22°15'S 43°37'E	MO, EA, FT, K, TAN
	Olson 697	Madagascar: Tulear: cultivated in town of Tulear	Watered garden	23°20'S 43°40'E	MO, EA, FT, K, TAN
<i>M. longituba</i>	Olson 704	Kenya: Northeastern Province: Mandera District: c. 20 km WNW of Mandera near locality of Filqo	Low hillside in dry scrub on rocky soil	3°58'11"N 41°45'00"E	MO, EA, FT, K
	Olson 708	Kenya: Northeastern Province: Wajir District: c. 20 km N of Wajir	Wooded grassland on deep soil	2°10'44"N 40°07'11"E	MO, EA, FT, K
	Olson 712	Kenya: Northeastern Province: Wajir District: c. 30 km E of Wajir	Wooded grassland on deep soil on or near limestone outcrops	1°44'01"N 40°15'36"E	MO, EA, FT, K

continued

APPENDIX 1 *continued*

Species	Collector and #	Locality	Habitat (when more than one collection has been made per sp., listed from dry to moist)	Latitude and longitude	Herbaria with vouchers
<i>M. oleifera</i>	Olson s.n.	India: Tamil Nadu: Padappai: Chengalpet District: c. 45 km W of Chennai	Cultivated tree in garden	c. 13°10'N 79°49'E	MO, EA, FT, K
<i>M. ovalifolia</i>	Olson 716 and 718	Namibia: Namib-Naukluft Park: W of Kuiseb Pass	Very rocky hillside	23°19'53"N 15°38'57"E	MO, WIND
<i>M. peregrina</i>	Olson 567	Oman: northern region: Wadi Muaydin 2-3 km N of Birkat Al Mawz	Rocky limestone hillside	22°54'N 57°40'E	MO, EA, FT, K
<i>M. pygmaea</i>	Nugent 25	Somalia: N: 13 km E of Qardho airstrip	"Grass and shrubs on alluvial plain"	9°33'N 49°19'E	EA
	Glover & Gilliland 1194	Somalia: N Coast near Berbera	"On hill above pool on Tug"	10°07'N 45°12'E	EA, K
<i>M. rivae</i>	Olson 677	Kenya: Eastern Province: Marsabit District: E slope of Baio Mtn	Rocky hillside in tall scrub	1°46'06"N 37°33'51"E	MO, EA, FT, K
	Olson 701	Kenya: Northeastern Province: Mandera District: c. 4 km N of Rhamu	Deep alluvial soil in remnants of low tropical deciduous forest/fields	3°55'26"N 41°11'37"E	MO, EA, FT, K
<i>M. ruspoliana</i>	Olson 703	Kenya: Northeastern District: Mandera District: on Kenya-Somalia border S of Dawa River	Disturbed grassy woodland on low limestone plateaus	3°57'31"N 41°52'36"E	MO, EA, FT, K
	Olson 702	Kenya: Northeastern District: Mandera District: Rhamu-Dimtu Division: around village of Yabicho	Below lip of low limestone plateaus in open tropical deciduous forest	3°56'28"N 41°10'00"E	MO, EA, FT, K
<i>M. stenopetala</i>	Olson 675	Kenya: Rift Valley Province: Baringo District: Parmalok Island, Lake Baringo	Grassy lower slopes of rocky island in lake	0°42'21"N 36°01'34"E	MO, EA, FT, K

APPENDIX 2
QUANTITATIVE MEASUREMENTS

Species/ class	Col. no.	VL	VD	VW	VG	VM	CA	FL	FD	FW	VS	MH	MW	UH	P:U:S
<i>arborea</i>	714a	311.50	129.20	5.33	2.36	12.58	0.18	833.70	35.95	2.09	3.04	330.60	3.14	158.00	61:21:18
	714b	nc	151.50	4.99	2.00	10.62	0.17	nc	nc	1.97	nc	nc	nc	nc	nc
<i>borziana</i>	678	294.70	60.50	2.96	2.52	39.25	0.20	nc	nc	2.62	2.32	362.00	2.44	189.00	45:25:31
	707	212.30	95.20	3.65	1.72	19.25	0.14	582.40	33.25	2.35	nc	nc	nc	nc	nc
<i>concanensis</i>	700a	nc	130.80	4.18	1.74	11.51	0.18	nc	nc	3.29	nc	nc	nc	nc	81:17:2
	700b	261.40	191.40	4.94	2.08	2.80	0.07	763.30	46.85	3.34	3.04	345.60	2.24	169.60	nc
<i>drouhardii</i>	695	238.10	167.90	5.76	1.56	7.62	0.20	nc	nc	2.35	nc	nc	nc	nc	83:10:7
	695a	nc	139.80	3.82	1.64	2.74	0.08	nc	nc	2.47	nc	302.40	2.72	105.00	nc
	695b	nc	129.20	3.89	1.40	5.75	0.11	nc	nc	2.40	3.40	nc	nc	nc	nc
	694	247.90	129.50	4.61	1.76	5.89	0.11	962.50	54.05	2.38	nc	nc	nc	nc	nc
	679	293.20	203.40	4.61	2.20	5.25	0.14	996.00	43.08	2.35	3.76	209.55	3.48	108.30	nc
	696	293.70	176.38	3.67	1.68	4.06	0.11	nc	nc	2.35	2.80	248.40	4.36	125.70	nc
<i>hildebrandtii</i>	693	266.40	185.00	3.86	1.44	1.38	0.03	nc	nc	1.78	nc	nc	nc	nc	100:0:0
	697a	269.20	105.10	3.07	1.96	2.11	0.05	788.50	60.50	2.52	4.08	419.10	3.32	210.60	nc
	697b	nc	170.70	3.41	1.56	2.98	0.06	nc	nc	2.04	3.92	406.80	nc	246.80	nc
	697c	nc	198.80	nc	1.68	2.55	0.13	nc	nc	nc	nc	nc	nc	nc	nc
<i>longituba</i>	704a	242.40	76.70	2.45	2.60	28.11	0.14	679.80	27.43	2.42	2.80	1724.00	2.88	217.30	15:16:69
	704b	nc	62.90	2.35	1.56	55.66	0.17	nc	nc	2.28	nc	nc	nc	nc	nc
	708	204.20	81.61	2.62	1.52	17.93	0.10	nc	nc	1.66	nc	nc	nc	nc	nc
	712	nc	96.10	2.78	2.16	17.62	0.15	nc	nc	1.73	2.36	355.20	3.08	123.60	nc
<i>oleifera</i>	s.n.	277.90	154.74	2.90	1.96	5.28	0.09	593.80	50.05	2.14	3.40	234.30	2.88	135.60	88:11:1
<i>ovalifolia</i>	716	205.80	112.70	3.98	1.64	17.28	0.18	nc	nc	1.38	nc	nc	nc	nc	nc
	716	nc	135.50	4.54	1.60	13.28	0.20	445.50	39.77	1.80	nc	nc	nc	nc	nc
	718	nc	113.10	4.27	1.80	16.60	0.12	nc	nc	2.81	nc	nc	nc	nc	89:8:3
	718a	203.90	123.60	3.31	1.64	9.72	0.11	nc	nc	2.28	3.24	474.00	3.56	98.69	nc
<i>peregrina</i>	567a	305.70	115.70	4.08	1.48	9.98	0.11	636.10	41.30	2.16	3.04	329.70	2.36	127.20	85:10:5
	567b	nc	nc	3.07	nc	nc	nc	nc	nc	nc	nc	309.00	nc	nc	nc
<i>pygmaea</i>	G&G 1194	276.80	42.50	3.22	2.40	65.85	0.17	nc	nc	2.54	2.64	452.70	2.08	165.00	24:30:46
	Nugent 25	170.30	56.68	2.90	2.84	54.22	0.26	429.90	31.07	1.20	2.80	486.56	2.00	>1500	41:32:27
<i>riuae</i>	677	263.10	81.10	4.78	1.56	14.28	0.07	nc	nc	2.57	nc	nc	nc	nc	72:22:6
	701	235.50	141.60	3.67	1.76	9.81	0.12	697.90	34.83	2.95	2.80	628.50	2.48	171.60	nc
<i>ruspoliana</i>	702	259.30	136.90	3.82	1.60	10.34	0.14	nc	nc	2.30	3.04	459.00	3.96	160.80	52:27:21
	703	nc	111.20	3.89	1.68	14.91	0.15	661.80	44.90	2.11	2.56	462.60	3.08	128.80	nc
<i>stenopetala</i>	675	256.00	149.20	6.82	1.60	13.21	0.17	696.40	51.90	1.73	2.76	183.90	2.04	nc	81:16:3
	675a	252.90	125.51	2.86	1.48	7.92	0.09	nc	nc	2.28	nc	nc	nc	149.70	nc
Bottle		252.71	147.84	4.16	1.67	7.40	0.12	777.78	49.86	2.19	3.42	320.59	2.78	149.26	88:8:3
Sarcorhizal		312.87	120.26	4.21	2.10	20.03	0.17	747.75	40.42	2.20	2.88	417.40	3.39	149.20	56:24:20
Slender		272.44	129.40	3.66	2.09	12.58	0.11	664.40	46.07	2.26	2.37	304.65	2.49	144.13	85:13:3
Tuberous		237.41	79.49	3.14	2.06	32.20	0.15	597.50	31.64	2.23	2.62	668.16	2.49	394.42	39:25:36

Means of quantitative measurements are summarized here for all 13 *Moringa* species and the four habit classes. Species are listed alphabetically. Collection numbers are Olson collection numbers unless otherwise specified; locality and voucher information is presented in App. 1. Figures are means of 25 measurements with the exception of LF dimensions, for which $n = 100$. Means for life form classes (bottle trees, followed by sarcorhizal trees, slender trees, and tuberous shrubs) are given in the last four rows of the table. Abbreviations: VL=vessel element length in μm ; VD=vessel element diameter in μm ; VG=vessels/group; VM=vessel density in vessels mm^{-2} ; CA=conductive area in $\text{mm}^2\text{mm}^{-2}$; VW=vessel wall thickness in μm ; FW=libriform fibre wall thickness in μm ; FL=libriform fibre length in μm ($n = 100$); FD=libriform fibre diameter in μm ($n = 100$); VS=vasicentric axial parenchyma cells/strand; MH=multiseriate ray height in μm ; MW=multiseriate ray width in number of cells; UH=uniseriate ray height in μm ; P:S:U=percentage of procumbent (P), square (S), and upright (U), and upright cells in multiseriate rays; nc=not counted.

APPENDIX 3

DISTRIBUTION OF RHOMBOIDAL CRYSTALS AND DRUSES

	<i>ar</i>	<i>bo</i>	<i>co</i>	<i>dr</i>	<i>hi</i>	<i>lo 704</i>	<i>lo 708</i>	<i>ol</i>	<i>ov</i>	<i>pe</i>	<i>py</i>	<i>ri</i>	<i>ru</i>	<i>st</i>
						<i>& 712</i>								
Xylem: RC in rays	+	+	-	+	+	+	+	+	+	+	+	+	+	+
Xylem: RC in LF's	+	-	-	occ	-	-	-	-	+	-	+	+	-	-
Xylem: RC in PP	+	occ	-	1	occ	-	-	-	+	n/a	-	occ	-	+
Xylem: RC in VP	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xylem: Ds in rays	occ	-	occ	+	+	-	+	-	-	-	+	+	+	-
Xylem: Ds in LF's	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Xylem: Ds in PP	-	-	occ	+	-	-	-	-	-	n/a	-	occ	-	+
Xylem: Ds in VP	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Pith: RC	occ	-	-	+	-	occ	-	-	+	+	+	+	-	+
Pith: Ds	+	+	-	+	+	+	+	+	+	-	+	+	+	+
Bark: RC in phelloderm	occ	-	occ	X	+	occ	-	+	+	occ	-	X	-	-
Bark: Ds in phelloderm	+	+	+	occ	+	+	+	+	+	occ	+	+	+	occ
Bark: RC in cortical P	+	+	occ	2	2	+	-	-	+	2	2	occ	+	X
Bark: Ds in cortical P	+	+	occ	+	+	+	+	-	+	+	+	+	+	+
Bark: RC in cortical sclerenchyma	+	occ	+	+	+	occ	-	+	+	+	n/a	+	+	+
Bark: Ds in cortical sclerenchyma	+	-	+	+	occ	occ	occ	-	-	-	n/a	-	+	+
Bark: RC in phloem rays	+	+	3	occ	occ	-	-	+	+	+	+	+	-	+
Bark: Ds in phloem rays	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Bark: RC in phloem	occ	-	+	-	occ	-	-	-	+	-	-	-	+	+
Bark: Ds in phloem	occ	occ	-	-	occ	-	-	-	-	occ	-	-	-	+
Bark: Ds in phloem P	n/a	-	+	occ	-	occ	-	-	-	+	n/a	n/a	+	n/a
Bark: RC in phloem P	n/a	-	+	occ	occ	-	-	-	-	+	n/a	n/a	+	n/a

Abbreviations are as given in the Methods section, with the addition of the following symbols and abbreviations: D=druses; RC=rhomboidal crystals; +=present; -=absent; occ=occasional (less than 25 in a given section); 1=present in parenchyma cells adjacent to fibres within 1-2 cells; 2=in cells adjacent to sclereids; 3=in cells adjacent to phloem fibres; n/a=cell type not identified in a given section; X=rhomboidal crystals transitional to druses (see Figs 102 and 105). *ar*=*arborea*; *bo*=*borziana*; *co*=*concanensis*; *dr*=*drouhardii*; *hi*=*hildebrandtii*; *lo 704*=*longituba 704*; *lo 708 & 712*=*longituba 708 & 712*; *ol*=*oleifera*; *ov*=*ovalifolia*; *pe*=*peregrina*; *py*=*pygmaea*; *ri*=*rivae*; *ru*=*ruspoliana*; *st*=*stenopetala*.