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SHORT COMMUNICATION

NEAR-VESSELLESSNESS IN EPHEDRA AND ITS SIGNIFICANCE

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ABSTRACT

Wood of two specimens of *Ephedra* from high alpine localities is nearly vesselless: *E. gerardiana* from 4,750 m in Tibet, and *E. rupestris* from 4,300 m in Argentina. *Ephedra gerardiana* from lower elevations in the Himalayas has more vessels, although even there they are not abundant. Instances in other species of *Ephedra* in which extensive areas of latewood or even entire growth rings are vesselless are cited; these tend to occur in high deserts with climates somewhat less extreme than those of the alpine localities. Near-vessellessness is interpreted as an adaptive condition in which the proportion of tracheids, conductively safer than vessel elements, reaches a maximum. Near-vessellessness in *Ephedra* wood is probably reversible within limits, and should be likened to production of latewood to the exclusion of earlywood. Comparisons are offered to dicotyledons in which abundance of vessels is lowered with respect to ecological extremes.

DURING A SURVEY of comparative wood anatomy of the genus *Ephedra* (Ephedraceae) as a whole, I discovered two samples, representing two species, in which vessels were nearly absent. One of these species, *E. gerardiana* Wall. ex Stapf, occurs in the Himalayas from Afghanistan to Nepal, upland Indian provinces, and Tibet; it can be found from 2,700 to 4,350 m (Stapf, 1889; Riedl, 1963). The other species, *E. rupestris* Benth., ranges from Ecuador through Peru and Bolivia to Tucuman Province, Argentina and can be found from 3,700 m to 5,000 m (Stapf, 1889; Hunziker, 1949). These two species reach higher elevations than do other species of *Ephedra* (Stapf, 1889).

The nearly vesselless specimen of *E. gerardiana* is from the highest elevation for which this species is known, 4,350 m. Wood of this specimen was compared with that of a specimen from a lower elevation, 2,700 m.

Comparisons of wood of *Ephedra* species other than *E. gerardiana* and *E. rupestris* are offered here because of growth ring phenomena in the genus. The absence or scarcity of vessels in latewood of *Ephedra* was noted earlier (Carlquist, 1980). Because this phenomenon seems related to near-vessellessness, manifestations of latewood vessellessness in *Ephedra* were sought. Comparisons to dicotyledons in which a lowered abundance of vessels can be

related to ecological extremes seems appropriate and is included in the discussion.

MATERIALS AND METHODS—Most wood samples were available in dried condition as portions of herbarium specimens. These samples are not, as one might think, merely twigs, for some herbarium specimens of *Ephedra* consist of entire plants, some with stems of near-optimal diameter for the species represented. Acknowledgment for such herbarium samples is offered to Dr. Juan Hunziker of the Instituto Darwinion (SI), to Dr. Nancy Morin of the Missouri Botanical Garden (MO), and to Dr. Kit Tan of the Edinburgh Botanical Garden (E). In addition, liquid-preserved wood samples of *Ephedra* were available as a result of my field work in the southwestern United States.

Nomenclature of *Ephedra* in the Old World follows that of Stapf (1889) and Riedl (1963); names of New World taxa are in accord with Cutler (1939) and Hunziker (1949).

Specimens cited and their localities are *E. breana* Phil., Bartlett 20555 (MO), Sierra de Los Colorados, Depto. Iglesia, Prov. de San Juan, Argentina; *E. coryi* Reed var. *viscida* Cutler, Carlquist 15831 (RSA), Tuba City, Arizona, 1950 m; *E. gerardiana*, Ludlow et al. 4074 (E), between Kala and Samada, U Province, southeastern Tibet, 4,700 m; *E. gerardiana*, Polunin et al. 884 (E), Jumea, Nepal, 2,700 m; *E. rupestris* Benth., Hunziker et al. 10504 (SI), ladera entre Molina y Mina Aguilar, Depto. Humahuaca, Prov. Jujuy, Argen-

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tina, 4,300 m. The Tibetan specimen of *E. gerardiana* is a small shrub dwarfed by browsing; the other specimens are of normal size for their respective species. Vessel presence in species not mentioned may be assumed to fall within normative limits for the genus, and these species will be cited in a subsequent monograph.

Wood was sectioned on a sliding microtome. Sections were stained with safranin and lightly counterstained with fast green. Sections of the Tibetan *E. gerardiana* were difficult to obtain because rays are composed of thin-walled parenchyma and tend to fracture, separating sections into segments. Macerations were prepared with Jeffrey's fluid and stained with safranin.

RESULTS—The wood (Fig. 1) of the collection of *E. gerardiana* from a high elevation in Tibet (Fig. 1) contains few vessels. The tracheary elements with wider diameter at the beginning of growth rings are mostly wide tracheids, and the only probable vessel element in the field shown is indicated with an arrow. The determination of whether cells are vessels or tracheids was made by studying both sections and macerations. In *Ephedra* perforations of vessels have much-reduced borders, whereas pits are fully bordered. This has been confirmed with SEM studies of wood of various *Ephedra* species (Carlquist, unpublished); what appear to be perforations occasionally still bear complete pit membranes as seen under SEM. Thus, light-microscope identifications of vessel elements, if inaccurate at all, may err on the side of claiming more numerous vessels than actually exist. The number of vessels in the wood of the Tibetan *T. gerardiana* can be expressed as between one and four per fascicular area (the woody cylinder, approximately 6 mm in diameter, is dissected into about twenty major fascicular areas separated by thin-walled ray cells).

In *E. gerardiana* from lower elevations in Nepal, vessels were found to be much more common than in the Tibetan collection, but even so, fewer per mm² than in the average *Ephedra* wood.

The other nearly vesselless wood of *Ephedra* studied is that of *E. rupestris* (Fig. 2-4). The portion successfully sectioned is an area about four times the area of the photograph shown in Fig. 2, and in that section only the two vessels indicated by arrows were observed. Careful study of macerated wood revealed only two vessel elements, both of which were photographed (Fig. 3, 4). In both of these, perforations form a single row, a characteristic which

contrasts with the usual multiseriate nature of perforations on *Ephedra* vessel elements.

For purposes of comparison and discussion, two woods of *Ephedra* were selected. In *E. coryi* var. *viscida* (Fig. 3), vessels are confined to a fraction of the growth ring, and the extensive latewood is vesselless. In the stem of *E. breana* illustrated (Fig. 6), vessels are scarce or absent in the first two or three growth rings.

DISCUSSION AND CONCLUSIONS—Although the samples studied are few, the scarcity of vessels in wood of high-alpine *Ephedra* woods is clearly demonstrated. The precise number of vessels per wood sample is of less significance than the relative scarcity of vessels and the ecological correlations of that scarcity. Conceivably, one could find some plants in high-elevation populations of the two species studied in which more numerous vessels occur, and one could perhaps find depauperate individuals that are wholly vesselless.

Attention was called earlier (Carlquist, 1980) to the paucity of vessels in latewood of *E. californica* Wats. This tendency is shown here even more strikingly for *E. coryi* var. *viscida* (Fig. 5). The section illustrated for *E. breana* shows the capability in the genus for formation of occasional growth rings devoid of vessels or nearly so, although production of vessels is clearly evident in the growth ring at the top of the photograph (Fig. 6). Analysis of wood of these and other species of *Ephedra* leads to the following conclusions about *Ephedra* wood: 1) latewood contains fewer vessels than earlywood; 2) latewood or even entire growth rings may lack vessels; and 3) relative abundance of vessels is a feature, modifiable to a degree, related to seasonal availability of soil moisture.

Scarcity of vessels undoubtedly is related to scarcity of water, whether due to drought or freezing. However, in terms of the physiological significance of *Ephedra* wood patterns, one should read vessel scarcity in terms of tracheid abundance. The conductive safety of latewood in which tracheids are present and vessels are scarce or absent was hypothesized earlier (Carlquist, 1980). The conductive safety of tracheids as compared to vessels lies in the ability of pit membranes to confine air bubbles within single cells; in vessels, air bubbles can spread the length of the vessel disabling it.

It tracheid abundance (vessel paucity) in latewood connotes conductive safety, one should expect this in areas of drought due to low soil moisture and in areas of physiological drought (water unavailability due to freezing of soil moisture). The former is certainly characteristic of desert areas where *Ephedra* grows.

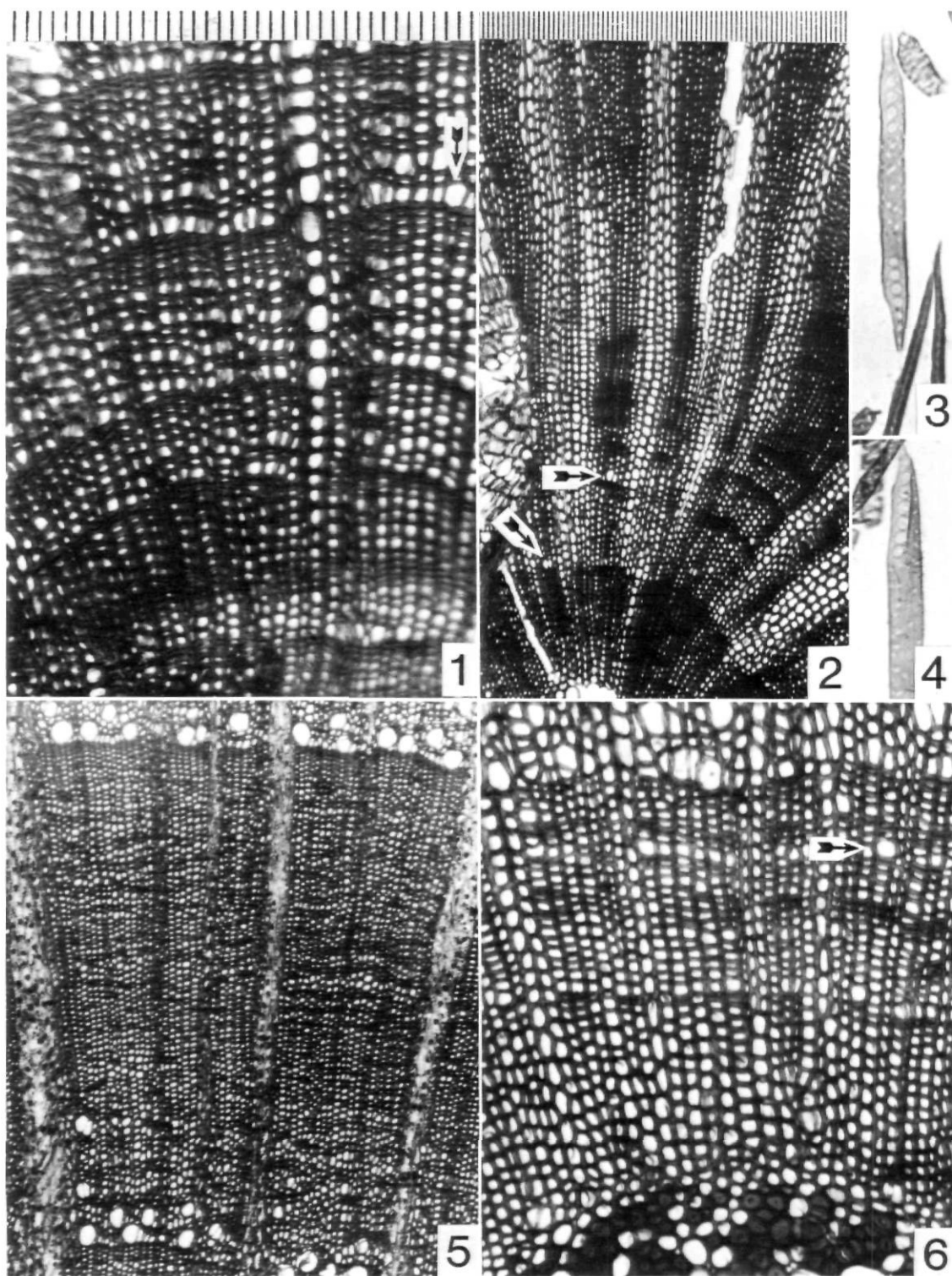


Fig. 1-6. Wood of *Ephedra* stems. 1. *Ephedra gerardiana*, Ludlow et al. 4074, transection (arrow indicates the only probable vessel in field). 2-4. *Ephedra rupestris*, Hunziker et al. 10504. 2. Transection (arrows indicate the only probable vessels in field). 3, 4. Vessel elements from macerations. 3. Vessel element with four perforations at each end. 4. Vessel element with six perforations at end. 5. *Ephedra coryi* var. *viscida*, Carlquist 15831, transection showing vessels restricted to a small portion of the growth ring. 6. *Ephedra breana*, Bartlett 20555, transection (pith containing gelatinous fibers below), showing first growth rings nearly vesselless (first probable vessel indicated with arrow). (Fig. 1, 3, 4, 6, magnification scales above Fig. 1 [divisions = 10 μ m]; Fig. 2, 5, magnification scale above Fig. 2 [divisions = 10 μ m].)

Many species of *Ephedra* certainly occupy high deserts (as in the case of *E. breana* and *E. coryi* var. *viscida*) where winter freezing is severe. The *Ephedra* species studied here, native to very high alpine deserts, would seem to represent the most extreme habitat possible in terms of adaptation by means of wood xeromorphy. In the Californian flora, wood adaptation by alpine shrubs shows a higher degree of xeromorphy than that shown by desert shrubs (Carlquist and Hoekman, 1985), although the Californian alpine region is probably moister than the desert alpine areas where *E. gerardiana* and *E. rupestris* grow. The wood of these two species can be considered as latewood produced to the exclusion of earlywood. Nocturnal freezing can be expected even during the growing season in the habitats of these two species.

Alpine deserts must represent the most extreme environment in which vascular plants exist, yet even in this habitat, vessels have not been extinguished in *Ephedra*, perhaps because the presence of a few narrow vessels does not lessen survival; narrow vessels embolize less readily than wide ones (Ellmore and Ewers, 1985). This circumstance is of potential significance with relation to Young's (1981) idea that in angiosperms woody vesselless groups such as Winteraceae have become secondarily vesselless. Vessels have been reduced in abundance (but not extinguished, as implied by Young, 1981) in certain Cactaceae and Crasulaceae (Bailey, 1966; Gibson, 1973). Increase in vascular (or vasicentric) tracheids in smaller cacti is doubtless related to succulence (tracheids with helical bands can expand and contract) rather than to xeromorphy per se. For Young's hypothesis to be operative, one would have to imagine adaptation to ecological regimes in ways that would lead to loss of vessels. For example, a phylad of now-vesselless woody dicotyledons would have had to have entered environments at least as extreme as the most extreme *Ephedra* habitats, lose vessels there entirely, then shifted to highly mesic sites (to which all now vesselless woody dicotyledons are now restricted) without leaving a single

species in any intermediate habitat—an incredible evolutionary feat. Alternatively, a phylad of now-vesselless woody dicotyledons would have had to have gone through a phase as aquatic herbs that had lost vessels, followed by a sudden return to woodiness and invasion of forest habitats—an equally implausible scenario. Young (personal communication) believes there may be other scenarios for loss of vessels in woody vessel-bearing groups, although he has not yet specified these.

Near-vessellessness in *Ephedra* is a reduction based on ecological factors, and is probably easily reversible; it should be considered in the nature of a production of latewood to the exclusion of earlywood. Although wood of such extreme character was not known to Bailey, it is not an exception to the trends of vessel evolution Bailey (1944) promulgated.

LITERATURE CITED

- BAILEY, I. W. 1944. The development of vessels in angiosperms and its significance in morphological research. *Amer. J. Bot.* 31: 421-428.
- . 1966. The significance of reduction of vessels in the Cactaceae. *J. Arnold Arb.* 47: 288-292.
- CARLQUIST, S. 1980. Further concepts in ecological wood anatomy, with comments on recent work in wood anatomy and evolution. *Aliso* 9: 499-553.
- , AND D. A. HOEKMAN. 1985. Ecological wood anatomy of the woody southern California flora. *IAWA Bull., n.s.*, 6: 319-347.
- CUTLER, H. C. 1939. Monograph of the North American species of the genus *Ephedra*. *Ann. Missouri Bot. Gard.* 26: 373-424.
- ELLMORE, G. S., AND F. W. EWERS. 1985. Hydraulic conductivity in trunk xylem of elm, *Ulmus americana*. *IAWA Bull., n.s.*, 6: 303-317.
- GIBSON, A. C. 1973. Comparative anatomy of secondary xylem in Cactoideae (Cactaceae). *Biotropica* 5: 29-65.
- HUNZIKER, J. H. 1949. Sinopsis de las especies del genero "*Ephedra*." *Lilloa* 17: 147-174.
- RIEDL, H. 1963. Ephedraceae. In K. H. Rechinger [ed.], *Flora Iranica* (pp. 1-8 of its own fascicle). Akademische Druck- und Verlagsanstalt, Graz, Austria.
- STAPF, O. 1889. Arten der Gattung *Ephedra*. *Denkschr. Math.-Nat. Classe Kais. Akad. Wiss. Wien* 56: 1-112.
- YOUNG, D. A. 1981. Are the angiosperms primitively vesselless? *Syst. Bot.* 6: 313-330.