1978

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Gibson, Arthur C. (1978) "Woody Anatomy of *Platyopuntias*," *Aliso: A Journal of Systematic and Floristic Botany*. Vol. 9: Iss. 2, Article 8.

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WOODY ANATOMY OF PLATYOPUNTIAS

Arthur C. Gibson

Introduction

Recent anatomical surveys of secondary xylem in Cactaceae (Gibson, 1973, 1975, 1977a, 1977b) have revealed that stem woods of unrelated species with convergent growth habits from all three subfamilies are strikingly similar. The tallest arborescent cacti, found in subfamily Cactoideae, have the longest vessel elements and libriform fibers and the shortest species not only have very short vessel elements but also may lack libriform fibers entirely and have scanty secondary thickenings on lateral walls of vessel elements. Within the broad diversity of vegetative forms in Cactaceae, the structure of secondary xylem is closely correlated with habit, so that an investigator may predict with good accuracy the qualitative and quantitative features of a wood even prior to examination. This close correlation between habit and xylem structure strongly suggests that natural selection has influenced the evolution of cactus woods.

To complete the survey of cactus woods data are needed on xylem structure of platyopuntias, those species of subfamily Opuntioideae with strongly flattened stems (pads), presently assigned in conservative treatments to *Opuntia* Miller subgenus *Opuntia* (Hunt, 1967; Benson, 1969), including the segregate genera *Brasilopuntia* (K. Schum.) Berger, *Consolea* Lem., and *Nopalea* Salm-Dyck. Platyopuntias, whose woods have been briefly described (Metcalf and Chalk, 1950; Conde, 1975), are ideal for habitat comparisons because they range in size from tall arborescents with large trunks to plants 1 dm tall that have no main stem and produce little secondary xylem. Even within a single series, e.g., *Opuntiae* of North America and the West Indies, one may find a wide range in sizes, and this size range occurs in both North and South America, each continent having its own indigenous series of the subgenus. Moreover, platyopuntias are ecologically interesting because species occupy a wide variety of habitats in the Western Hemisphere, including all types of desert and dry lowland regions, coastal strand, grassland, tropical scrub and rain-green forest, oak woodland, and coniferous forest. The purpose of this paper is to describe the woods of platyopuntias, to compare their woods with those of other cacti, and to determine whether habit or habitat shows any direct relationship to the wood structure of platyopuntias.

Materials and Methods

Most wood samples for this study were collected in the field, including fresh materials graciously donated by Drs. G. L. Benny, D. E. Boufford, R.

H. Hevly, M. C. Jefferson, J. W. Kimbrough, and P. D. Sorensen. Cultivated materials were collected from the Boyce Thompson Southwestern Arboretum, Superior, Arizona, and the Huntington Botanical Gardens, San Marino, California, and dried wood samples were obtained from the wood collections of Harvard University, Cambridge, and the U.S. Forest Products Laboratory, Madison. Voucher specimens were prepared for all live collections and deposited in the University of Arizona Herbarium, Tucson (ARIZ). All specimens were labeled as to the position of the sample within the plant (Table 1) because intraplant differences in cactus woods are highly significant (Gibson, 1977b).

All living materials were preserved in 70% formalin-acetic-alcohol fixative (Johansen, 1940). Because most woods of platyopuntias are composed of alternating zones of lignified axial elements and broad, unlignified vascular rays, relatively few samples could be sectioned in bulk by sliding microtomy. Instead, standard paraffin methods were used to prepare microscope slides of all succulent woods, and the thickness of sections varied with the nature of the material. Sections were stained with safranin and fast green. Macerations were prepared by Jeffrey's method (Johansen, 1940) and stained with safranin. Techniques for obtaining quantitative data for axial elements were those used in previous wood studies (Gibson, 1973, 1977b). Terminology of anatomical structures in general follows standardized nomenclature for woods and Bierhorst (1960) for secondary thickenings.

The major growth habits of platyopuntias, with the abbreviation used for each in Table 1, are as follows. Arborescent forms, mostly 4–6 m tall, have a massive trunk and strong, typically ascending or arching primary branches (Arb.). Height of some species may exceed 10 m, e.g., *O. argentina* of northern Argentina and *O. echios* var. *gigantea* of the Galapagos Islands. Shrubs may be erect with a definite trunk and strong primary branches (Shr. I), arching or trailing from a short trunk (Shr. II), or decumbent (Shr. III). Many fruticose species exhibit within their geographical ranges all three growth habits, and arborescent species also have fruticose forms. Some desert and grassland species are caespitose with essentially no trunk, and primary branches rest on the ground or are partially buried by soil (Caesp.). Such caespitose forms rarely exceed 4 dm in height. Most highly reduced in size are suffrutescent forms (Suffr.) in which pads are relatively short lived and frequently produce adventitious roots, thus facilitating multiplication of plants when portions of the plant die back in dormant periods.

Observations

Accumulation of secondary xylem is directly proportional to the height of the plant. A radius of wood in lower stems of arborescent species often exceeds 4 cm whereas that of suffrutescent species may be less than 3 mm in an old specimen. Increases in wood accumulation are attributable to

Table 1. Wood characteristics of platyopuntias.

TAXON	Growth habit (see text)	Vessel elements		Lateral wall ^b	Libriform fibers			
		Mean length (μm)	Mean diameter (μm) ^a		Mean length (μm)	Mean diameter (μm)	Maximum wall thickness (μm)	Fiber/vessel element length
<i>Napalea auberi</i> (Pfeiff.) Salm-Dyck	Arb.							
Gibson 3136 Trunk		269	88.2	Sc-Tr	829	46.6	4.4	3.08
<i>N. cochenillifera</i> (L.) Salm-Dyck	Arb.							
SJRw 19527 Outer Trunk		305	70.1	Sc-Tr	828	37.8	4.4	2.71
Inner Trunk		395	61.1	Sc-Tr	793	37.8	4.4	2.01
<i>Opuntia</i> subg. <i>Opuntia</i>	Caesp.							
Series <i>Basilares</i>								
<i>O. basilaris</i> Engelm. & Bigel.								
Gibson 3111 Lower Stem		120	47.9/24.4	Hel-Tr	none			
Small Adventitious Root		297	26.8	Sc-Alt	498	27.6	2.3	1.68
Gibson 3158 Lower Stem		116	42.3/21.2	Hel-Tr	none			
Small Adventitious Root		218	35.2	Tr-Alt	424	21.4	1.8	1.94
<i>O. microdasys</i> (Lehm.) Pfeiff.	Shr. II							
Gibson 3150 Lower Stem		132	54.1	Sc-Tr	455	40.7	4.1	3.45
<i>O. rufida</i> Engelm.	Shr. I							
Gibson 3200 Trunk		138	76.0	Tr-Alt	588	52.2	6.0	4.26

^a Two numbers signify means for earlywood and latewood, respectively, in ring-porous xylem.^b Bordered pitting alternate (Alt), transitional (Tr), or scalariform (Sc); secondary thickenings reticulate (Ret) or helical (Hel).^c Observations for these features are not available because of microtechnical problems encountered in these mucilaginous specimens.

Table 1. Continued.

TAXON	Growth habit (see text)	Vessel elements		Lateral wall ^b	Libriform fibers				
		Mean length (μm)	Mean diameter (μm) ^a		Mean length (μm)	Mean diameter (μm)	Maximum wall thickness (μm)	Fiber/vessel element length	
Series <i>Curassavicae</i>									
<i>O. drummondii</i> Graham	Suffr.								
Boufford 15946 Lower Stem		88	32.6/14.6	Hel-Ret	n.a. ^c	23.2	2.6	n.a.	
Small Adventitious Root		205	30.8	Sc-Alt	372	23.2	2.9	1.81	
Series <i>Ficus-indicae</i>									
<i>O. ficus-indica</i> (L.) Miller	Shr. I–Arb.								
Gibson Branch		276	56.7	Tr-Alt	679	43.7	3.8	2.46	
Series <i>Macdougalianae</i>									
<i>O. atropes</i> Rose	Arb.								
Gibson 3139 Trunk		287	90.5	Sc-Tr	931	46.6	5.8	3.24	
<i>O. bravoana</i> Baxter (= <i>O. wilcoxii</i> ?)	Shr. II								
Jefferson Lower Stem		179	55.0	Sc-Alt	630	40.1	4.4	3.52	
Small Adventitious Root		290	67.8	Tr-Alt	495	34.9	2.9	1.71	
<i>O. cantabrigiensis</i> Lynch	Shr. I								
Gibson 3141 Trunk		242	74.2	Sc-Alt	838	52.4	4.1	3.46	
Branch		186	53.5	Sc-Tr	n.a.	34.9	4.1	n.a.	

Table 1. Continued.

TAXON	Growth habit (see text)	Vessel elements		Lateral wall ^b	Libriform fibers			
		Mean length (μm)	Mean diameter (μm) ^a		Mean length (μm)	Mean diameter (μm)	Maximum wall thickness (μm)	Fiber/vessel element length
Series <i>Opuntiae</i> (incl. <i>Dillenianae</i> , <i>Phaeacanthae</i> , <i>Setispinae</i> , and <i>Tortispinae</i>)								
<i>O. azurea</i> Rose	Shr. I							
Gibson 3142	Trunk	167	66.6	Sc-Tr	715	34.9	4.4	4.28
	Branch	133	72.2	Sc-Tr	562	31.9	4.4	4.23
	Main Root	183	70.1	Tr-Alt	712	39.3	5.8	3.89
<i>O. chlorotica</i> Engelm. & Bigel.	Shr. I							
Gibson 3110	Trunk	163	57.3	Tr-Alt	577	32.0	4.9	3.54
<i>O. humifusa</i> (Rafinesq.) Rafinesq. (= <i>O. compressa</i>)	Suffr.							
Boufford 15945	Subterranean Stem	133	32.3/16.7	Ret-Tr	n.a.	24.7	2.9	n.a.
	Small Adventitious Root	243	26.8	Tr-Alt	438	23.3	2.3	1.80
Gibson 3354	Lower Stem	142	32.6/14.6	Ret	none			
<i>O. lata</i> Small	Suffr.							
Gibson 3148	Lower Stem	115	24.2	Ret	rare	29.1	2.6	n.a.
<i>O. lindheimeri</i> Engelm.	Shr. I							
Gibson 2967	Trunk	207	75.4/30.6	Alt	826	34.9	5.2	3.99

Table 1. Continued.

TAXON	Growth habit (see text)	Vessel elements		Lateral wall ^b	Libriform fibers			
		Mean length (μm)	Mean diameter (μm) ^a		Mean length (μm)	Mean diameter (μm)	Maximum wall thickness (μm)	Fiber/vessel element length
<i>O. lindheimeri</i> var. <i>linguiformis</i>								
(Griffiths) L. Benson		Shr. II-III						
Gibson 2939	Lower Stem	158	55.9/42.2	Alt	575	33.5	5.5	3.64
	Lower Branch	156	61.4/26.2	Alt	616	37.8	5.8	3.95
	Upper Branch	184	44.8	Tr-Alt	609	37.8	6.0	3.31
	Small Adventitious Root	266	53.5	Tr-Alt	574	28.5	3.8	2.16
<i>O. littoralis</i> (Engelm.) Cocker. var. <i>martiniana</i> (L. Benson) L. Benson								
Gibson 3157	Lower Stem	153	64.0/26.5	Tr-Alt	541	36.8	4.7	3.54
<i>O. macrorhiza</i> Engelm.								
Gibson 3152	Lower Stem	154	31.1/16.0	Ret	none			
	Succulent Main Root	174	34.0/16.6	Hel-Ret	n.a.	20.4	3.2	n.a.
	Small Adventitious Root	206	47.1	Tr-Alt	392	32.0	4.1	1.90
<i>O. macrorhiza</i> var. <i>pottsii</i> (Salm-Dyck)								
L. Benson		Shr. II						
Gibson 3201	Lower Stem	182	66.9	Sc-Alt	619	45.0	4.4	3.40

Table 1. Continued.

TAXON	Growth habit (see text)	Vessel elements		Lateral wall ^b	Libriform fibers			
		Mean length (μm)	Mean diameter (μm) ^a		Mean length (μm)	Mean diameter (μm)	Maximum wall thickness (μm)	Fiber/vessel element length
<i>O. phaeacantha</i> Engelm. var. <i>discata</i> (Griffiths) L. Benson & Walkingt.								
Gibson 2820	Lower Stem	194	58.5/27.1	Alt	598	40.7	4.7	3.08
	Small Adventitious Root	247	26.5	Alt	450	26.2	2.9	1.82
<i>O. phaeacantha</i> var. <i>major</i> Engelm.								
Gibson 2960	Outer Lower Stem	146	51.2/30.0	Tr-Alt	679	34.8	5.2	4.65
	Inner Lower Stem	157	57.6/44.2	Sc-Alt	638	33.7	4.9	4.07
	Lateral Root	261	57.3/31.7	Tr-Alt	676	34.8	4.4	2.59
<i>O. tapona</i> Engelm.								
Gibson 3004	Lower Stem	203	75.7/55.9	Sc-Alt	660	42.1	3.2	3.25
<i>O. violacea</i> Engelm. var. <i>gosseliniana</i> (Weber) L. Benson								
Gibson 3010	Lower Stem	156	67.8	Tr-Alt	555	43.5	5.2	3.55
	Lateral Root	250	46.9	Tr-Alt	637	30.6	4.1	2.55
<i>O. violacea</i> var. <i>macrocentra</i> (Engelm.) L. Benson								
Gibson 2965	Lower Stem	125	47.7	Ret-Alt	580	33.5	5.2	4.64
	Succulent Main Root	144	40.4	Ret-Alt	525	37.8	4.2	3.65
	Small Adventitious Root	249	46.6	Tr-Alt	525	30.6	2.9	2.11

Table 1. Continued.

TAXON	Growth habit (see text)	Vessel elements		Lateral wall ^b	Libriform fibers			
		Mean length (μm)	Mean diameter (μm) ^a		Mean length (μm)	Mean diameter (μm)	Maximum wall thickness (μm)	Fiber/vessel element length
Gibson 2970	Lower Stem	131	64.6	Tr-Alt	529	34.1	4.6	4.04
Gibson 2971	Lower Stem	136	57.6/24.4	Tr-Alt	629	32.0	4.6	4.63
	Lateral Root	260	64.3	Tr-Alt	538	30.6	4.1	2.07
<i>Opuntia</i> sp.								
Gibson 2982a	Trunk	177	86.4	Tr-Alt	724	43.5	6.1	4.09
Series <i>Palmadorae</i>								
<i>O. palmadora</i> Britt. & Rose								
Gibson 3094	Trunk	182	49.2	Sc-Tr	560	40.7	4.1	3.08
Series <i>Piliferae</i>								
<i>O. pilifera</i> Weber								
Gibson 3123	Trunk	237	87.9	Sc-Tr	713	58.2	6.7	3.01
Series <i>Polyacanthae</i>								
<i>O. erinacea</i> Engelm. & Bigelm.								
Gibson 3155	Lower Stem	156	54.4/21.0	Ret-Alt	573	25.4	2.3	3.67
	Branch	140	37.8/13.9	Hel-Ret	none			
	Main Root	154	56.7	Alt	505	31.9	1.7	3.28
<i>O. fragilis</i> Nutt.								
Gibson 3193	Subterranean Stem	198	46.0	Sc-Alt	367	29.0	6.1	1.85
Hevly	Lower Stem	120	55.9/16.0	Hel-Ret	none			
	Small Lateral Root	301	45.7/27.1	Sc-Alt	n.a.	30.5	2.6	n.a.

Table 1. Continued.

TAXON	Growth habit (see text)	Vessel elements		Lateral wall ^b	Libri-form fibers				
		Mean length (μm)	Mean diameter (μm) ^a		Mean length (μm)	Mean diameter (μm)	Maximum wall thickness (μm)	Fiber/vessel element length	
<i>O. polyacantha</i> Haw. var. <i>trichophora</i> (Engelm. & Bigel.) Coult.									
Gibson 2964	Lower Stem	Caesp.	142	45.4/21.0	Ret-Alt	none			
	Branch		131	47.6/21.8	Sc-Alt	rare	25.5	2.9	n.a.
	Lateral Root		192	56.5/24.9	Alt	492	43.5	2.9	2.56
Series <i>Pumilae</i>									
<i>O. pumila</i> Rose									
Gibson 3135	Lower Stem	Shr. II	162	74.8	Tr-Alt	494	55.1	4.1	3.05
	Branch		177	53.5	Sc-Alt	529	37.7	3.2	2.99
	Large Lateral Root		189	65.4	Tr-Alt	533	37.7	3.2	2.82
	Young Lateral Root		270	60.8	Tr-Alt	520	37.7	2.9	1.93
Series <i>Robustae</i>									
<i>O. robusta</i> Wendl.									
Gibson 3145	Lower Stem	Shr. I-II	144	59.4	Ret-Tr	450	40.7	4.6	3.13
Series <i>Spinossimae</i> (incl. <i>Consolea</i>)									
<i>O. moniliformis</i> (L.) Haw.									
SJRw 8981	Trunk	Arb.	432	90.5	Tr-Alt	1,050	58.2	5.2	2.43

Table 1. Continued.

TAXON	Growth habit (see text)	Vessel elements		Lateral wall ^b	Libriform fibers			
		Mean length (μm)	Mean diameter (μm) ^a		Mean length (μm)	Mean diameter (μm)	Maximum wall thickness (μm)	Fiber/vessel element length
Series <i>Sulphuræ</i>								
<i>O. pampeana</i> Speg.		Shr. III						
Gibson 3028	Lower Stem		176	53.5	Hel-Tr	none		
	Small Adventitious Root		244	39.9	Tr-Alt	563	30.6	3.5
								2.31
<i>O. sulphurea</i> G. Don								
Gibson 3065	Lower Stem	Shr. III–Caesp.	113	50.3	Hel-Tr	none		
Series <i>Tomentosæ</i>								
<i>Opuntia</i> cf. <i>tomentosa</i> Salm-Dyck		Arb.						
Gibson 3117	Trunk		266	76.5	Sc-Tr	811	56.7	6.7
								3.05
Series <i>Tunæ</i>								
<i>O. depressa</i> Rose		Shr. III						
Gibson 3124	Lower Stem		157	49.2	Sc-Alt	n.a.	33.5	3.5
								n.a.
<i>O. tuna</i> (L.) Miller								
Yw 7662	Branch?	Shr. I–Arb.	175	102	Sc-Tr	745	55.3	6.4
Yw 7663	Trunk		259	71.9	Sc-Tr	862	46.8	5.2
								4.31
								3.33

Table 1. Continued.

TAXON	Growth habit (see text)	Vessel elements			Libriform fibers			
		Mean length (μm)	Mean diameter (μm) ^a	Lateral wall ^b	Mean length (μm)	Mean diameter (μm)	Maximum wall thickness (μm)	Fiber/vessel element length
Species incertae sedis								
<i>O. macbridei</i> Britt. & Rose	Suffr.–Caesp.							
Gibson 3192 Lower Stem		134	34.9	Ret-Tr	n.a.	27.6	2.0	n.a.
<i>O. quimilo</i> K. Schum.	Arb.							
Gibson 3058 Trunk		281	79.7	Tr-Alt	838	49.5	5.2	2.98

more and wider growth layers. Woody cylinders are generally bilaterally flattened, their shapes corresponding to that of the pads, and the pith is typically very elongate in transection. Nearly cylindrical stems, as in *O. palmadora* and *O. pumila*, have relatively narrow cylinders of wood and narrow pith.

Platyopuntias have normal stem and root secondary growth produced by a single vascular cambium. Fascicular cambium forms first but shortly a cambial ring develops by formation of ray initials in interfascicular regions. To the unaided eye, rays produced by interfascicular cambium appear to be part of primary growth because cells have only unligified primary walls and mucilage cells often differentiate within these rays. In most platyopuntias, cells with lignified secondary walls are produced only from fascicular cambium; consequently, first-formed secondary xylem follows exactly anastomosing patterns of primary shoot fasciculation (see Gibson, 1976), and elaborate networks of lignified xylem are protracted long distances into secondary growth (Figs. 1, 2). As in other dicotyledons, ray initials of very wide interfascicular regions are gradually transformed into fusiform initials adjacent to fascicular cambium, thereby decreasing the size of these unligified "primary rays" (sensu Barghoorn, 1940). Only in very large growth habits, e.g., the largest arborescent species, are most primary rays converted into fully lignified secondary xylem (Figs. 3, 4), leaving only a small unligified zone in the woody cylinder associated with each areole. Large fruticose and arborescent species initially have relatively small primary rays because the reticulum of primary vascular bundles has more numerous accessory bundles.

The terms fibrous and nonfibrous have been used (Gibson, 1973, 1977b) to describe secondary xylem in which fibers are present or absent, respectively. Erect shrubs and trees have fibers in the first-formed secondary xylem of stems, but fruticose species with arching or decumbent stems frequently exhibit nonfibrous xylem in inner growth layers and fibrous xylem in outer ones. Nonfibrous woods occur in stems of platyopuntias with low growth habits. In outermost xylem, fibers occur only in the last growth layer in *O. drummondii*, *O. erinacea*, and *O. lata* and one specimen of *O. humifusa*, and fibers are completely absent in lower stems of seven species belonging to four series (Table 1). However, even within the outer growth layer of a single stem marked variation is observed. Wedges of axial xylem that originate opposite axial and leaf-trace bundles of the primary vascular system are widest and may have fibers whereas those opposite the branch-trace and accessory bundles are more narrow and often lack fibers. Within an individual plant fibers may be present in lowermost stems but absent in branches, and roots typically possess fibers, especially in the innermost xylem, even though stems may lack fibers entirely. Succulent main roots of *O. humifusa*, *O. macrorhiza*, and *O. violacea* var. *macrocentra* show poor

Figs. 1-4. Woods of arborescent platypuntias.—1. Dried, decorticated old pad of *Nopalea auberi*, showing intricate network of lignified secondary xylem and regions where succulent tissues are present.—2. Same from main stem of *Opuntia pilifera*.—3-4. Wood sections of *N. cochenillifera*.—3. Transection, showing fully lignified, diffuse-porous wood.—4. Tangential section; vascular rays are multiseriate. (3-4 $\times 25$)

development of fibers in comparison with less succulent main, lateral, and adventitious roots of these same or other species.

Growth rings.—Many stem woods of platypuntias exhibit anatomical growth rings. In outer xylem of fruticose and many arborescent species, dense clusters of fibers are generally separated by regions of unlignified fusiform parenchyma cells, forming discrete growth layers (Figs. 5-8). Each fibrous zone probably corresponds to a flush of pads produced on that shoot. Within these unlignified zones vessels are generally slightly wider

Figs. 5-8. Fibrous stem-wood transections of platyopuntias.—5. *Opuntia atropes*, small arborescent.—6. *O. rufida*, erect shrub.—7. *O. lindheimeri* var. *linguiformis*, low shrub.—8. *O. fragilis*, suffrutescent subshrub. Note the decrease in amount of lignified xylem, width of axial xylem, and cluster size of libriform fibers (lf) with decrease in plant height. Only *O. atropes* has regions of lignified vascular rays (lvr), whereas smaller species have unlignified vascular rays (uvr), often with abundant druses (dark structures). (All $\times 20$)

and in larger clusters than in the fibrous zones, which are sometimes devoid of vessels. Ring porosity is fairly pronounced in nonfibrous xylem (Figs. 9-13; Table 1) but generally is not as discernible in fibrous xylem within the same stem. Stems of tall arborescent species (Fig. 3) and of *O. palma-*

dora and *O. pumila*, species with nearly cylindrical stems, lack sharply delimited growth rings in outer wood where fully lignified vascular rays are present.

Root woods of platyopuntias lack distinct growth rings but are occasionally semi-ring porous (Figs. 14, 15). Young lateral and adventitious roots sometimes show series of false annual rings where concentric zones of fibers are poorly lignified.

Platyopuntias lack interxylary cork, a feature present in lower stems of many North American cylindropuntias (Gibson, 1977b).

Vessel elements.—Mean vessel-element length from stems of platyopuntias range from 432 to 88 μm . The longest vessel elements are found in arborescent species; trunk woods of all arborescent specimens ($n = 10$) have mean vessel-element lengths greater than 200 μm . These trunkwood means fit within the range of lengths observed in Cactoideae with comparable size (Gibson, 1973) but are slightly greater than those in *Pereskioopsis* Britt. & Rose and significantly greater than those in cylindropuntias of North and South America, the stock from which the platyopuntias were undoubtedly derived (Gibson, 1977b). Vessel elements in lower stems of fruticose species are shorter, ranging from 242 to 125 μm ($n = 24$). Conde (1975) also observed that two fruticose species have mean vessel-element lengths within this range. Caespitose and suffrutescent species have extremely short vessel elements, ranging from 156 to 88 μm ($n = 11$), excluding a very old, fibrous, subterranean stem of *O. fragilis* growing in cultivation ($\bar{x} = 198 \mu\text{m}$). Within each series tall, erect plants tend to have the longest vessel elements. Vessel elements are generally longer in woods of lower stems than in the branches of the same individual, but the reverse is sometimes also true.

Adventitious and narrow lateral roots of platyopuntias have relatively long vessel elements, the means ranging from 301 to 192 μm ($n = 17$), whereas those of main roots, including succulent ones, range from 189 to 144 μm ($n = 5$). Within an individual plant vessel-element length is always greatest in the small lateral or adventitious roots, and these values are significantly greater than those in the main root. A similar trend was recorded in cylindropuntias (Gibson, 1977b).

Mean vessel diameter in platyopuntias is relatively small ranging from 102 to 24.2 μm (Table 1). In diffuse-porous stem woods, the widest vessels occur in arborescent species, and mean vessel diameters roughly decrease with a decrease in plant height and erectness, thus paralleling trends in vessel-element length. However, some erect shrubs have vessels wider than arborescent forms, so correlations between plant height and vessel diameter are not perfect. In ring-porous stem woods, mean diameters of earlywood vessels range from 75.7 to 31.1 μm , the widest ones occurring in the largest growth habits and the narrowest ones occurring in nonfibrous secondary xylem. Ring porosity is generally not observed in plants over 1.5 m tall.

Figs. 9–13. Stem transections of small caespitose platyopuntias.—9–10. Non-fibrous secondary xylem.—9. *Opuntia polyacantha* var. *trichophora* of Texas, showing ring porosity in outer growth layers.—10. *O. pampeana* of Argentina, showing poor differentiation of growth layers and vascular tracheids (vt) distributed throughout axial xylem. This figure also illustrates axial xylem in radial view, in which annular rings of vascular tracheids and scanty secondary thickenings of vessels may be observed.—11–13. *O. basilaris*—11. First-formed vascular tissues; vascular tracheids with wide annular bands occur in the pith and within and adjacent to primary xylem (px), in which few vessels are present. Widest vascular tracheids occur on the edges of the xylem.—12. Inner secondary xylem, where vessel diameters distinguish earlywood (ew) and latewood (lw) and widest vascular tracheids occur along the margins of axial xylem.—13. Outermost secondary xylem, where ring porosity is still observed but vascular tracheids are absent. Unlignified vascular rays (uvr) have druses (d). (All $\times 45$)

Latewood vessels are about half the diameter of earlywood vessels and show a similar decrease in diameter with a decrease in plant height. Within a stem mean diameters of earlywood and latewood vessels increase annually, whereas mean diameters in diffuse-porous woods remain relatively constant from innermost secondary xylem. Vessel diameters vary greatly within a single growth layer, being widest in the widest wedges of axial xylem and narrowest in the minor ones.

Depending on the age of the root, vessels may be wider or narrower than those at the base of the stem. In typical roots with abundant wood fibers, vessel diameter increases markedly in the first several millimeters of secondary growth (Figs. 14, 15) until the diameter is approximately the same as in the lower stem. Succulent roots have extremely narrow vessels, present only in narrow wedges of axial xylem radiating from the pith (Figs. 16, 17).

In platyopuntias, vessels occur independently or in small or large groups or clusters. A high percentage of vessels are solitary in stem woods of arborescent species (Figs. 3, 5), and average vessel grouping tends to increase with a decrease in plant height. Moreover, vessel density in axial xylem also increases with a decrease in plant height, and in latewood of ring-porous woods vessel clusters are very large, sometimes having many files of narrow elements that experience little, if any, cell enlargement.

Where stem woods exhibit alternating zones of wood fibers and unlignified parenchyma in axial xylem, vessel grouping is greatest in unlignified zones, and vessels may be scanty or completely absent in the fibrous zones (Figs. 6, 7). No measurements are available to make interspecific comparisons of total vessel area in stem transections. Vessel grouping tends to be low and density very high in small roots with abundant wood fibers (Figs. 14, 15), whereas vessel groups are small but very widely spaced in succulent roots.

As in all Cactaceae, vessel elements in both primary and secondary xylem have simple perforation plates. In platyopuntias, orientation of perforation plates may be nearly transverse to diagonal, even within a single specimen. Generally, the longest elements tend to have the most inclined end walls and short, pitted tails.

Lateral-wall pitting tends to be highly variable, even within an individual plant, so the range of pitting types for each specimen is indicated in Table 1. On the relatively long, wide vessel elements in stems of arborescent platyopuntias, lateral walls have elongate, broadly scalariform or transitional pits with thin borders (Fig. 18). Stem woods of fruticose species have mostly transitional and alternate pitting; for example, those of series *Opuntiae* have mostly alternate pitting, but the transitional intervacular pitting is observed in the narrowest vessels or those that occur adjacent to or surrounded by unlignified parenchyma. The greater the amount of unlignified cell walls present in secondary xylem the less one finds vessel-to-vessel

Figs. 14-17. Root transections of platypuntias.—14. *Opuntia violacea* var. *gosseliniana*; main root, showing axial xylem with libriform fibers (lf) separated by unlignified vascular rays (uvr) with druses (dark structures).—15. *O. polyacantha* var. *trichophora*; lateral root, showing fibrous axial xylem and unlignified vascular rays with mucilage cells (mc). Note high vessel density and faint growth layers where libriform fibers are abundant.—16. *O. macrorhiza*; succulent main root lacking a pith with abundant mucilage cells in unlignified vascular rays.—17. *O. humifusa*; succulent root having a large pith (p). In *O. humifusa*, libriform fibers occur only in the innermost secondary xylem of each narrow wedge of axial xylem. (All $\times 20$)

alternate pits with full borders. Nonfibrous stem woods generally have vessels with helical or reticulate secondary thickenings in inner growth layers (Fig. 19) and transitional pitting in outermost growth layers. Pitting types change gradually throughout secondary growth; one can observe first-formed elements with transitional pitting (Fig. 20), which show the reticulate first-order framework of the secondary wall (*sensu* Bierhorst and Zamora, 1965). Throughout this secondary xylem pit borders are often eliminated where vessels contact parenchyma cells. Vessels without bordered pits do not occur in last-formed xylem where fibers appear.

Thickest vessel walls are found in species with the widest vessels and also in the widest vessels within a specimen. Vessels surrounded by unlignified parenchyma generally have thicker and better lignified walls than those found within a matrix of libriform wood fibers.

Tyloses and resinous deposits are absent from vessels of platyopuntias.

Vascular tracheids.—Vascular tracheids of platyopuntias are nonliving, imperforate, broadly fusiform cells with wide annular, rarely annular-helical bands of secondary wall (Figs. 10, 21), similar to those of other Opuntioideae (Gibson, 1977b). These cells occur in nonfibrous xylem or rarely in fibrous woods of roots, where they are present only in the unlignified vascular rays. Stem vascular tracheids generally have two to five rings. Those present in roots generally have more numerous annular bands and are longer and narrower than those in the stem of the same plant. Annular bands may be 25 μm thick; consequently, the lumen in narrow elements through these rings may be only several micra wide.

Vascular tracheids first appear in ground tissue adjacent to and inside primary xylem after protoxylem is functional (Fig. 11). In caespitose species vascular tracheids are particularly abundant in pith ground tissue where their differentiation from parenchyma cells continues after secondary growth begins. Vascular tracheids differentiate in the unlignified rays of secondary growth and in axial xylem. They are more numerous and widest in ray cells adjacent to axial xylem and less abundant, often scarce, and extremely narrow in the center of axial xylem (Fig. 12). In platyopuntias maximum diameter of vascular tracheids is 100 μm . Vascular tracheids decrease in number from inner to outer secondary xylem, disappearing first within axial xylem and finally on the edges of axial xylem with vessels have bordered pits. As a rule vascular tracheids do not occur after wood fibers are present, although occasionally one or two may be observed in unlignified zones.

In platyopuntias, vascular tracheids are abundant in stems of small growth habits, especially those with completely nonfibrous secondary xylem, and these cells decrease in abundance with an increase in plant height so that most arborescent species completely lack these cells in secondary xylem.

Figs. 18-21. Cell types of stem axial xylem.—18. *Nopalea cochenillifera*; longitudinal view of vessel (v) with bordered, elongate lateral-wall pits. $\times 140$.—19. *Opuntia basilaris*; radial view of vessels with reticulate secondary thickenings. $\times 160$.—20. *O. erinacea*; vessel in secondary xylem, showing borders deposited inside reticulate thickenings. $\times 285$.—21. *O. polyacantha* var. *trichophora*; vascular tracheids (vt) distributed next to vessels with scanty secondary walls. $\times 85$.

This result is expected because pitted vessels are present in the first-formed secondary xylem. Elimination of vascular tracheids in secondary xylem is paralleled by their elimination in primary xylem and ground tissue. An ideal example is series Basilares, in which *O. basilaris*, the smallest species, has abundant vascular tracheids in ground tissue, primary xylem, and numerous growth layers of secondary growth; *O. microdasys*, a small shrub, has some vascular tracheids in ground tissue, primary xylem, and the first several growth layers; and *O. rufida*, an erect shrub, has very few vascular tracheids, most of them in ground tissue.

Libriform fibers.—I previously showed that in Cactoideae (Gibson, 1973) mean fiber length in mature lower stem woods increases linearly with increase in plant height and erectness so that the tallest species have the longest fibers, exceeding $850\text{ }\mu\text{m}$ in length. Fruticose species have shorter fibers and epiphytes and small and weak growth habits have fibers less than $550\text{ }\mu\text{m}$ in length. *Cylindropuntias* do not show this trend (Gibson, 1977b), in part because maximum plant height of these taxa is 4 m and most species are 2 m tall or less. Mean length of libriform fibers in *cylindropuntias* ranges from 725 to $264\text{ }\mu\text{m}$. In *platyopuntias*, stem wood fibers are moderately to extremely short, ranging from $1,050$ to $367\text{ }\mu\text{m}$ (Table 1). Fibers greater than $700\text{ }\mu\text{m}$ are found in the arborescent species and large, erect shrubs ($n = 13$), and fiber length decreases with a decrease in plant height. Small growth habits have extremely short fibers or are nonfibrous; those speci-

mens where 50 measurements could not be taken of the fibers from macerations also have extremely short fibers, e.g., *O. drummondii* and *O. humifusa*. Within individual series, degree of erectness correlates closely with mean fiber length, but in some series, e.g., Opuntieae, the amount overlap of growth habits confuses the pattern. For these species greater sampling is desirable to determine the range of means for each species and for each growth habit within a single species. Differences in mean fiber lengths between lower stems and branches show no trends in absolute values.

Main roots of platyopuntias have fibers that are equal in length to those of the lower stem, but fibers of narrow lateral and adventitious roots are extremely short, ranging from 574 to 372 μm .

Because vessel-element and fusiform-initial length are approximately equal, differences in mean libriform-fiber and vessel-element lengths may be expressed as a ratio (Table 1) to represent proportional intrusive growth of fibers. This may be plotted to show also the quantitative differences in element lengths from each specimen (Fig. 22). Four lines arising from the ordinate show where the proportion of fiber to vessel-element length equals 1, 2, 3, and 4, and the further away from the origin the greater the differences in lengths of these elements. Length ratios in the lower stem range from 4.65 to 2.43, but when values of arborescent and fruticose species are separated, the range for tree species (3.33 to 2.43) is significantly different than that for smaller plants (4.65 to 3.05). Therefore, arborescent platyopuntias have relatively long stem fibers that experience the greatest amount of intrusive growth, but the ratios are smaller than those fruticose species that have shorter elements. Ratios determined from inner xylem are generally smaller than those of outer xylem. Length ratios in major roots range from 3.89 to 2.56 and overlap those of the lower stem, whereas those of narrow roots range from 2.31 to 1.68, the wider the root the greater the ratio. For each plant these same trends hold.

The old, subterranean stem of *O. fragilis* is noteworthy because the plot of axial-element lengths falls near those of adventitious roots (Fig. 22; arrow), not lower stems of caespitose species. This anomaly may be explained if roots and this stem grow in similar physical and physiological environments.

Evolutionary changes in fiber diameter and cell-wall thickness seem to accompany changes in fiber length. The longest libriform fibers tend to be relatively wide and have the thickest walls (Table 1), and decreases in fiber width and wall thickness parallel a decrease in fiber length. Exceptions to this are the species of *Nopalea*, which have relatively long but narrow fibers. Young roots have extremely narrow fiber with thin walls, and both cell diameter and wall thickness are greater in larger roots.

Libriform fibers of platyopuntias are always nucleate and long lived.

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Fig. 22. The relationship between mean lengths of libriform fibers to vessel elements for lower stems of fruticose species (open triangles), lower stems of arborescent species (solid triangles), major roots (solid circles), and narrow roots (open circles). Straight lines indicate where the ratio of lengths equals 1, 2, 3, and 4. Vessel-element lengths of nonfibrous stem wood (X) are shown. An arrow notes the anomalous value for a suffrutescent species, discussed in the text.

They frequently form one internal septum per cell, but septation is most conspicuous in woods of lower stems than in branches or roots. Most young roots lack septa entirely.

Axial parenchyma.—In zones where fibers are produced, distribution of axial parenchyma is scanty paratracheal. These cells are products of fusiform cambial derivatives that experience one or more transverse divisions. Succulent regions of axial xylem in fibrous and nonfibrous stem woods are mostly composed of nucleated fusiform parenchyma cells that lack secondary walls (Figs. 5–9). However, in *Opuntia fragilis* and *O. pampeana* cells that touch vessels have thin, un lignified secondary walls in regions where fibers are absent.

In platyopuntias, axial parenchyma generally does not store starch grains.

Vascular rays.—Because most ray initials of the first-formed interfascicular

cambium are never transformed to fusiform initials, stem woods of platyopuntias typically have only multiseriate primary rays throughout secondary growth (Figs. 6–13). In species less than 1.5 m tall, these rays lack secondary walls, and in radial view cell shape may be polyhedral, square, or upright. Upright cells are commonly found in the smallest growth habits, particularly in regions where vascular tracheids occur in rays and throughout secondary growth adjacent to axial xylem. Fruticose species tend to have more narrow rays also with unlignified primary walls, but one can observe patches of cells with lignified secondary walls, e.g., in *O. cantabrigiensis* and *O. rufida*, the taller the plant the greater the development of ray lignification. Cells of these rays are mostly square in radial view. Primary rays in arborescent species undergo considerable reduction in height and width as ray initials are converted to fusiform initials. Procumbent cells are particularly abundant in stem woods where the majority of ray cells have fully lignified secondary walls. These woods (Figs. 3, 4) resemble woods of arborescent Cactoideae (Gibson, 1973).

In roots of platyopuntias vascular rays are relatively narrow, very high, and multiseriate, and ray cells have only primary walls (Figs. 14–17). The unlignified primary rays radiate from the protostele. Only in large roots do secondary rays form within axial xylem by transformation of fusiform initials to ray initials. Roots of platyopuntias resemble young roots of Opuntioideae with cylindrical stems (Bailey, 1964; Gibson, 1977b) but are unlike main roots of chollas that have fully lignified rays. In radial view ray cells are generally square or upright; upright cells are found with vascular tracheids in small roots of the shortest growth habits. Succulent roots of platyopuntias have extremely wide vascular rays that form most of the secondary xylem. These ray cells are typically polyhedral and greatly enlarged, often producing abundant mucilage. Widely spaced mucilage cells may also be observed in unlignified rays of stems and roots of many species, but mucilage production in these structures appears to be very limited.

Druses are present in rays of stems and roots wherever cells lack secondary walls (Figs. 5–9, 11–13). Unlignified ray cells also are sites for accumulation of abundant starch grains in many species. Starch grains may be simple or compound.

Storied structure.—Unlike other cacti, storied is difficult to observe in most platyopuntias. The fusiform initials of the vascular cambium rarely show stratification, but where this is observed, the initials are arranged in diagonal, rather than horizontal, tiers.

Discussion and Summary

Level of specialization.—Woods of platyopuntias, like those of other Cactaceae, are highly specialized for dicotyledons, having relatively short, narrow vessel elements with simple perforation plates; libriform fibers that

are nucleate at maturity; scanty paratracheal axial parenchyma; and multi-seriate vascular rays with specialized characteristics. Lateral walls of vessels in outer secondary xylem may have scalariform or transitional pitting or even reticulate thickenings. Although these types of lateral-wall pitting might have been interpreted as primitive based on broad trends of xylem evolution (see Carlquist, 1961), Carlquist (1962) pointed out that xylem features commonly classified as primitive can occur in secondary xylem of some specialized dicotyledons, especially in succulent taxa. The occurrence of primary xylem features in woods, termed paedomorphosis by Carlquist, is clearly evident in these and other cacti (Gibson, 1973, 1975, 1977a, 1977b), and one should use the presence of multiseriate alternate pitting, which generally is found in first-formed secondary xylem in the roots, to estimate the true level of the specialization in platyopuntias. Moreover, the vascular cambium is highly specialized, having some stratification of fusiform initials even though stratification is more noticeable in other Opuntioideae.

Authors agree that platyopuntias are highly specialized taxa of subfamily Opuntioideae which must have evolved from stock with cylindrical stems. One expects that platyopuntias with nearly cylindrical stems, such as *O. pumila*, have retained some primitive features for subgenus *Opuntia*, but this assumption may lead to false comparisons. No phylogeny of these taxa has ever been proposed to define clearly phylads and primitive features; therefore, we cannot be certain that opuntias with flattened stems have evolved just once from plants with cylindrical stems. Xylem anatomy gives no aid in determining primitive features for each phylad because an investigator must make subjective, untestable choices to establish the starting point for xylem divergence.

Stem woods of platyopuntias, even those of many arborescent species, are more succulent than those of other Opuntioideae (Gibson, 1977b). In subgenus *Cylindropuntia*, a decorticated wood skeleton is relatively solid, interrupted only by large, unlignified primary rays opposite the tubercles. The solid portions have fully lignified axial and ray systems. In platyopuntias, unlignified rays are more evenly distributed throughout the secondary xylem, yielding the finely reticulate patterns for the lignified portions of wood. Furthermore, within axial xylem of many taxa, including small arborescent species, regions of wood fibers are replaced by fusiform axial parenchyma cells, often in large numbers. Consequently, succulence is more evenly distributed and in higher proportion than in woods of cylindropuntias. *Opuntia tunicata*, a cylindropuntia of series *Imbricatae*, has considerable succulence throughout secondary xylem much like the condition in platyopuntias. It is interesting that *O. tunicata* is more similar to *O. pumila*, a platyopuntia with nearly cylindrical stems, in many vegetative and reproductive features than any other cylindropuntia, and one should compare these two species in any future phylogenetic study. In *Pereskioopsis*

and, especially, *Quiabentia* Britt. & Rose succulence is present in the vascular rays and also in axial xylem (Bailey, 1964; Gibson, 1975). Neither of these taxa produces as much secondary xylem as found in arborescent and large fruticose platyopuntias. Woods of platyopuntias are also mesomorphic in that vessels are considerably wider than those in cylindropuntias, and woods of large growth habits are diffuse porous. In platyopuntias, vessels are never blocked by tyloses, even in ring-porous woods, and intervessel pits are large and generally have thinner borders than in subgenus *Cylindropuntia*.

Correlations with habit.—As in Cactoideae (Gibson, 1973), the structure of secondary xylem in stems of platyopuntias is closely correlated with habit. Changes in wood structure from the tallest arborescent through fruticose to small caespitose and suffrutescent species includes the following decreases in xylem features: 1) total amount of secondary xylem produced by reduction in the number and width of annual growth layers; 2) length and width of libriform fibers; 3) thickness of libriform-fiber walls; 4) number of libriform fibers within axial xylem; 5) degree lignification of vascular rays; and 6) thickness of vessel-element walls. These are changes in the mechanical properties of woods, signifying a decrease in mechanical strength of xylem for shorter plants. The complete absence of wood fibers in the smallest growth habits must be considered the ultimate stage in the reduction of xylem strength.

Plant erectness appears to be determined by the amount of mechanical support provided by wood and extraxylary succulence, as measured by the width and thickness of pads. Racine and Downhower (1974) showed that plant height and erectness correlate also with differences in growth rate and number of pads. These characters may be coupled so that fast-growing, robust, thick pads produce relatively strong secondary xylem, even in the first season. Presence of a wood skeleton within pads probably helps to keep stems erect during periods of water stress when succulent tissues lose turgor pressure. Species that experience long periods of water stress and lack fibrous stem woods, such as *Opuntia basilaris*, exhibit inrolling of pads with increased desiccation.

Pad size, morphology, and growth rate may play the determining role in ultimate plant height, so one expects and does find wide variations in pad morphology and growth habits over the geographical range of individual species. Growth habit can be effected not only by climatic factors but also by evolutionary factors, e.g., genetic drift and natural selection.

Whereas Cactoideae and platyopuntias show close correlations between wood strength and stem diameters with plant height and erectness, no clear habital correlations are found in Opuntioideae with cylindrical to globular stems (Gibson, 1977b). For these organisms I have proposed that diameters of upper stems are not suitable for a large arborescent design; the

cross-sectional area of branches would not be sufficient to support heavy succulent branches of a large tree, especially one with heavy fruits. Tallest arborescent cylindropuntias of North and South America are seldom 4 m tall, and most species are significantly shorter. One might suggest that evolution of arborescent opuntiods was promoted by flattening of stems, providing wider, potentially stronger branches. Opuntias with cylindrical stems have axial elements with similar dimensions as those of platyopuntias and Cactoideae with comparable height. Nonfibrous stem woods have evolved independently in North and South America in small growth habits with cylindrical to globular stems.

Other evolutionary trends correlating with plant height and erectness include changes in length and width of vessel elements, grouping of vessels, types of lateral-wall pitting between vessels, and presence and abundance of vascular tracheids. Stem woods of arborescent species have relatively long, wide vessel elements, low average vessel grouping, scalariform to transitional intervessel pitting, and few, if any, vascular tracheids. Fruticose species have short, relatively narrow vessel elements, relatively high vessel grouping, mostly transitional to alternate vessel-to-vessel pitting, and few to numerous vascular tracheids, restricted to innermost growth layers. Caespitose and suffrutescent species, which often lack libriform fibers in stems, tend to have ring-porous woods with extremely short, narrow vessel elements, high vessel grouping, reticulate to transitional pitting, and abundant vascular tracheids, particularly in the pith, primary xylem, and first-formed growth layers of secondary xylem. Having less secondary wall probably increases lateral water movement within a plant because more primary walls are exposed, but here the mechanical strength of secondary xylem is certainly decreased. These small plants are held erect mostly by turgor pressure of succulent tissues.

Intraplant variations in cell features.—An analysis of axial-element lengths in cylindropuntias (Gibson, 1977b) showed that when mean lengths of libriform fibers and vessel elements are expressed as a ratio those at the base of the plant ranged from 3.76 to 2.55; those in branches from 3.46 to 2.30; those in main roots from 4.00 to 3.15; and those in minor roots from 2.30 to 1.35. Plants that lack a main trunk have the smallest lower-stem ratios. For each plant the ratio is approximately the same or slightly higher in the fully lignified main root than in the trunk but is smaller in minor roots and branches than in the trunk. In platyopuntias, similar values are obtained (Table 1; Fig. 22): those at the base of the plant ranged from 4.65 to 3.05 for fruticose species and from 3.33 to 2.43 for arborescent species; those in main roots with unlignified rays or with abundant succulence ranged from 3.89 to 2.56; and those in minor roots ranged from 2.31 to 1.68. For each plant the ratio of the lower stem is approximately the same or slightly higher than in the main root but is significantly higher than in minor roots, the older the root the

higher the ratio. These data suggest there are underlying physiological factors influencing lengths of elements in opuntiods in addition to those correlated to plant height; in a plant part of a particular age, wood fibers experience a characteristic amount of intrusive growth, regardless of the species. For example, very young roots with less than 0.5 mm of secondary growth have relatively long fusiform initials (=vessel-element length) but little intrusive growth of fibers; older, somewhat succulent main roots have shorter fusiform initials and slightly more intrusive growth of fibers; and very old, fully lignified main roots have short fusiform initials and the greatest amount of intrusive growth of fibers. Therefore, because cell dimensions are influenced by position within a plant and age of the sample as well as by evolutionary factors, one should be wary in using these features in systematic treatments, as that attempted by Conde (1975). Speculation on the possible functional meanings of these intraplant differences as per Carlquist (1975) are unwarranted without a full understanding of the factors controlling dimensions of xylem derivatives. As I have pointed out (Gibson, 1977b), minor differences in xylem tensions between roots and lower stems in cacti or any other plants cannot by themselves account for marked differences observed in vessel-element lengths and grouping in stems and roots of an individual plant.

The ontogeny of nonfibrous stem woods may provide interesting data for understanding factors controlling wood evolution in Cactaceae and, perhaps, other plant families, especially those with shoot succulence. Vascular tracheids differentiate far from the meristematic regions producing new xylem cells: 1) vascular tracheids form in medullary ground tissue after primary xylem is mature; 2) they differentiate within primary xylem long after vessels are functional; and 3) even in secondary growth they differentiate to the inside of fully mature vessels and occur most commonly and are larger in the vascular rays. Moreover, vascular tracheids generally do not occur after libriform fibers are produced and are no longer found in xylem where vessels have bordered alternate pits; changes in vessel pitting coincide with the elimination of vascular tracheids and production of wood fibers. These observations suggest that levels and balances of growth substances influencing the differentiation of xylem cells change through time.

As I noted earlier (Gibson, 1977a, 1977b), various workers have provided evidence that auxin is important for fiber formation, and a full complement of phytohormones and sugars is needed for production of fully lignified secondary xylem. With this in mind, it is curious that in stems of platyopuntias major axial regions opposite abundant sieve tubes often have abundant wood fibers and minor axial regions opposite scanty conducting phloem have few fibers. In addition, vascular rays form lignified secondary walls only in the tallest species.

Synchronous changes in xylem cells types may mean that different bal-

ances of growth substances promote differentiation of a unique set of xylem features and, in time, "normal," fully lignified cell types are produced when a plant part receives proper levels of all growth substances. Bierhorst and Zamora (1965) have provided some evidence that secondary walls of vessels are deposited in two stages, the first-order framework of secondary thickenings and the second-order framework, which joins the first-formed gyres and produces bordered pits. That one can observe lateral walls transitional between reticulate and transitional in late nonfibrous secondary xylem lends some support to this hypothesis. This transition normally occurs in metaxylem of specialized dicotyledons. Perhaps what we are seeing in nonfibrous xylem of cacti is the separation of these processes. Deposition of the second-order framework may be delayed because important stimuli are lacking in juvenile plants. If this speculative, but hopefully testable, explanation is correct, the occurrence of paedomorphosis in woods (sensu Carlquist, 1962) will have clearer meaning, and we may judge whether nonfibrous wood in Cactaceae is a purposeful physiological adaptation.

Acknowledgments

This investigation was supported by National Science Foundation grant GB-37664. I am grateful to Prof. Ing. Armando T. Hunziker, Museo Botánico, Córdoba, Argentina, for providing invaluable field assistance.

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