

CLADODE JUNCTION REGIONS AND THEIR BIOMECHANICS FOR ARBORESCENT PLATYOPUNTIAS

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The three terminal cladode junction regions along branches of four arborescent platyopuntias—*Nopalea cochenillifera*, *Opuntia ficus-indica*, *Opuntia robusta*, and *Opuntia undulata*—were investigated for their reaction wood traits, flexural stiffness, and elastic moduli. The junctions had suberized tissue, phloem, wood, and pith and were surrounded by a collar composed of epidermis, hypodermis, and chlorenchyma. Gelatinous fibers, which were often associated with lignified axial parenchyma and vessels, occurred only in the wood of the two older junction positions for the three species with the most massive cladodes (the *Opuntia* spp.). Gelatinous fibers were more frequent in lateral regions, indicating that they are formed in response to large static loads and that they limit lateral movement of the branches. Axial parenchyma cells in regions under tension often stained lightly and had irregularly thickened walls. Pith eccentricity, which resulted from a greater wood extent in compressive than in tensile regions, occurred for all three positions for all four species, except for the youngest junctions of *O. robusta* and *O. undulata*. Greater wood extent in compressive regions may be because the wood is primarily made up of parenchyma, which resists compressive forces better than tensile forces. Flexural stiffness of junctions did not differ between bending parallel to the cladode face toward compressive regions versus bending perpendicular to the cladode face toward lateral regions but increased with increases in junction age, reflecting increases in junction cross-sectional area. Collars significantly resisted compressive stresses, accounting for 34% of junction flexural stiffness. Junction region elastic moduli varied among species but did not increase with junction age. Thus, the biomechanics for the cladode junctions of arborescent platyopuntias are affected mostly by the wood cross-sectional area and the resistance provided by the collar.

Keywords: biomechanics, cladode, gelatinous fibers, junctions, *Nopalea*, *Opuntia*, platyopuntias, reaction wood.

Introduction

Internal stresses resulting from the architecture of a tree often affect the anatomy of its branches. The trunks of trees that conform architecturally to Troll's model (Bell 1991), such as those of *Ulmus rubra*, *Plantanus orientalis*, and *Brownea ariza*, are comprised of sympodial units, which are vertical only in their most proximal region; the rest of the unit is plagiotropic (Fisher and Stevenson 1981; Mueller 1988; Bell 1991). A portion of the plagiotropic region secondarily re-orient to the vertical, which is usually accompanied by the development of tension wood on the upper side of a branch (Fisher and Stevenson 1981; Mueller 1988). The branches of opuntoid cacti are also comprised of sympodial units, with larger arborescent platyopuntias—opuntias with flattened stems termed “cladodes”—forming trunks that resemble those of nonsucculent trees (Gibson and Nobel 1986; Bobich and Nobel 2001a). The junctions connecting successive cladodes of platyopuntias also develop tension wood (Bobich and Nobel 2001a). However, platyopuntias differ from most woody dicotyledons with sympodial axes because the junction between

two cladodes is smaller in cross-sectional area than the rest of the cladodes (Nobel and Meyer 1990; Bobich and Nobel 2001a). Traits of tension wood, such as eccentric wood growth and ray dilation (Fisher and Stevenson 1981; Fahn 1990; Hejnowicz 1997), for cladode junctions of arborescent platyopuntias may be accentuated as a result of the concentration of stresses in the smaller cross-sectional area of the junctions.

The typical histological trait of tension wood is the presence of gelatinous fibers, which differ from typical fibers in that their secondary wall has a thick inner layer, the G-layer, with little or no lignin or hemicellulose (Fahn 1990). Microfibrils in the G-layer are aligned parallel to the longitudinal axis of the fibers, which may allow for contraction of the cell wall (Fahn 1990). Because of their cell wall characteristics and their location in regions experiencing tensile stresses, gelatinous fibers may be responsible for the secondary movement of branches (Fisher and Stevenson 1981; Fournier et al. 1994). Gelatinous libriform fibers occur in clusters in stem junctions of platyopuntias (Bobich and Nobel 2001a) and cylindropuntias (opuntias with cylindrical stems; Bobich and Nobel 2001b). However, the location of gelatinous fibers in junction wood with reference to tensile and compressive stresses and whether they can function in the secondary movement of the massive branches of platyopuntias are unknown.

Cactus stems have large amounts of thin-walled water-

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storage parenchyma cells in their pith and cortex (Gibson and Nobel 1986). The region of the upper cladode that surrounds the junction, here termed the “collar,” consists of epidermis, hypodermis, and cortical parenchyma (chlorenchyma). The secondary phloem and xylem have large amounts of thin-walled parenchyma cells (Gibson and Nobel 1986). In fact, many cactus growth forms totally lack fibers in their secondary tissues (Gibson 1973, 1978; Mauseth 1993). For *Opuntia ficus-indica*, *Opuntia littoralis*, and *Opuntia “occidentalis,”* the youngest cladode junctions are essentially fiberless, and fibers are much less frequent than axial parenchyma cells in older junctions (Bobich and Nobel 2001a). Because of the large amount of parenchyma cells in a junction, the elastic properties for bending in different directions will depend on the location of zones of cells with secondary cell walls (Kahn-Jetter et al. 2001).

In this study, four species of arborescent platyopuntias, all of which can exceed 3 m in height, were investigated to determine how whole plant and cladode morphology relate to the anatomy and, consequently, to the biomechanical properties of cladode junctions. Because parenchyma resists compressive forces better than tensile forces (Niklas 1992), the extent of cladode junction reaction wood was hypothesized to be greater for regions experiencing compressive stresses than for those experiencing tensile stresses. Furthermore, this asymmetry should be greater for species with more massive cladodes. Gelatinous fibers and lignified zones were hypothesized to occur primarily in regions experiencing tension, as for *Opuntia laevis* (Kahn-Jetter et al. 2001) and other dicotyledons (Fisher and Stevenson 1981). It was also hypothesized that the anatomical responses to gravity make junctions more resistant to bending along the axis experiencing maximal tensile and compressive stresses than in the axis perpendicular to the maximal stresses. Testing these hypotheses using biomechanical, morphological, and anatomical analyses will aid in understanding branch development for arborescent platyopuntias and other large plants with sympodial growth.

Material and Methods

Plant Material

Branches of *Nopalea cochenillifera* (L.) Salm-Dyck (accession number 1269 of Texas A&M University, Kingsville, Tex.), *Opuntia ficus-indica* (L.) Miller (accession number 1282), *Opuntia robusta* Wendland (accession number 1240), and *Opuntia undulata* Griffith (accession number 1276) were obtained from 10-yr-old plants at the Agricultural Experiment Station, University of California, Riverside. Branches consisted of four cladodes connected by three intervening cladode junctions (fig. 1A); the youngest to the oldest cladodes and their underlying junctions were referred to as “terminal,” “subterminal,” and “sub-subterminal.” The cladode angle from the vertical (α [degrees]; fig. 1A) for each cladode along a branch was measured in the field using a circular protractor and a plumb line. The axes parallel to the cladode faces for over half of the branches in the field were within 10° of vertical; “cladode angle” refers to the declination of the cladode longitudinal axis from vertical (fig. 1A). The regions of the cladode junction subjected to maximal tensile or compressive forces and the

intervening lateral regions (fig. 1B) were marked with a permanent marker on the cladodes in the field.

Deflection Measurements

Branches of each species were held in place by a wooden clamp that was covered with foam rubber to prevent damage to the lower cladode of a junction and bolted to a rigid scaffold (Bobich and Nobel 2001a; fig. 1C, 1D). Forces were applied to the distal part of the youngest cladode using a handheld force gauge (Shimpo Instruments, Itasca, Ill.) in two directions: (1) parallel to the cladode face toward the region of the junction experiencing maximum compressive stresses in the field (fig. 1C) and (2) perpendicular to the face of a cladode toward a lateral region (fig. 1D). A small amount of tissue was removed from the distal portion of the cladode (fig. 1C) to facilitate the application of forces and measurement of deflections parallel to the cladode face in the direction of the region experiencing compressive stresses (fig. 1B). Deflections were measured in triplicate using an electromechanical transducer (E-Line LVDT [linear variable differential transformer]; Shae-vitz Engineering, Pennsauken, N.J.) connected to a voltage amplifier and a chart recorder.

Bending for junctions without the resistance provided by the collar (fig. 1B) was determined for the terminal, subterminal, and sub-subterminal junctions for four branches of *O. robusta* after removing the collar for the upper cladode of a junction. The collar was eliminated by cutting 5 mm above the junction and removing all of the tissue external to the suberized tissue of the junction (fig. 1B). Forces were then applied parallel to the cladode face in the direction of the maximum compressive forces, as described previously.

Morphological and Anatomical Measurements

After the deflection measurements, the upper cladode was removed from the branch at the junction, and its length and mass were measured. The lengths of the junction axis experiencing the maximum tensile and compressive stresses and of the axis perpendicular to it were measured as well as the axial lengths for the regions containing the wood and pith and the pith alone (Bobich and Nobel 2001a). The extent of the wood (the distance from the first-formed secondary xylem to the vascular cambium) for the regions experiencing the maximum tensile and compressive stresses was determined using calipers for all three junctions.

Samples of the junction region were removed from four terminal, subterminal, and sub-subterminal cladode junctions for each species and analyzed anatomically. In addition, a collar and junction were cut into four sectors representing the tensile region, the compressive region, and the two intervening lateral regions, which had been labeled in the field (fig. 1B). The larger sectors were cut in half, resulting in eight sectors, two for each region. Hand sections ca. 50 μm thick were taken across every sector and stained on slides using 1% phloroglucinol followed by 25% (v/v) HCl or stained using 0.05% (w/w) toluidine blue in water for 30 s, rinsed with distilled water, and then wet mounted. Widths of the axial and the ray regions were measured near the vascular cambium (fully developed in all investigated junctions) using an ocular micrometer; the sections were magnified $\times 30$ with an Olympus BH-2 compound mi-

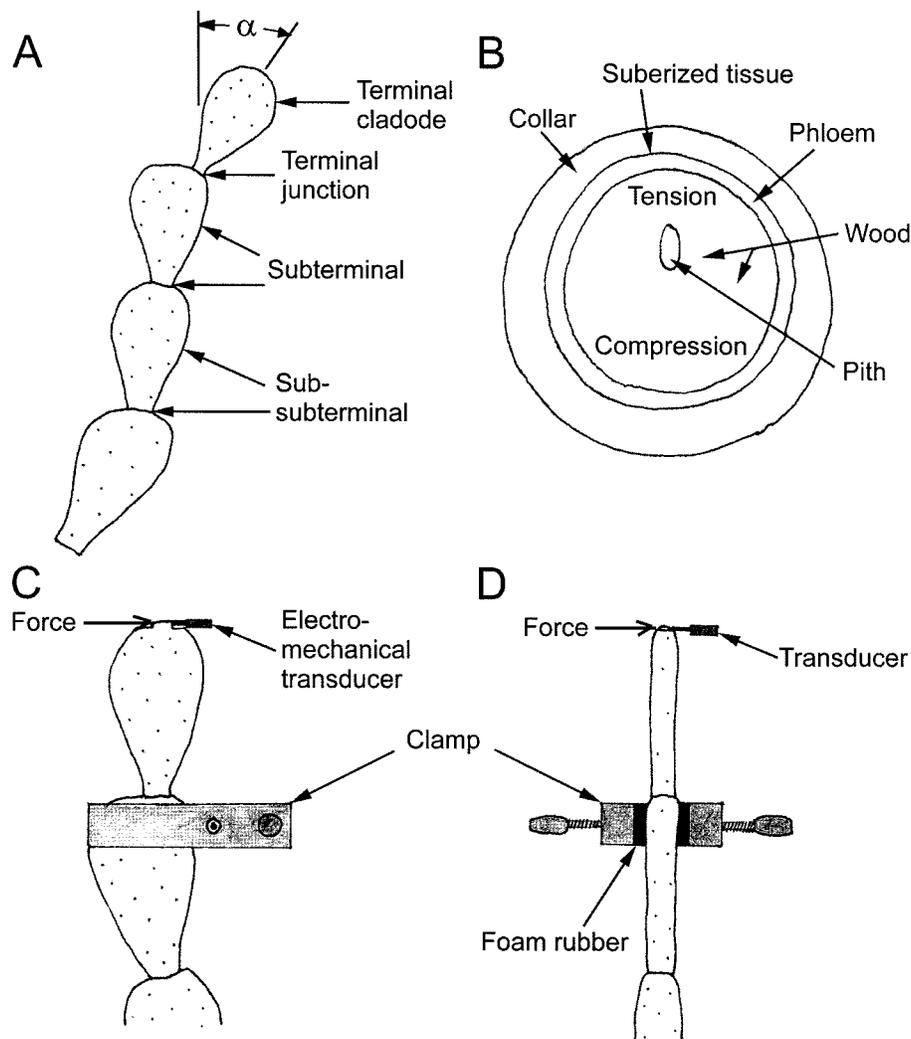


Fig. 1 A, Typical branch used for analysis and its cladode/junction nomenclature. B, Cladode junction regions analyzed; maximal tensile and compressive stresses in the field occur along the axis indicated, which is parallel to the faces of the upper cladode. C, Experimental arrangement for deflection measurements parallel to the cladode face toward the maximum compressive stresses experienced by the junction in the field. D, Experimental arrangement for deflection measurements perpendicular to the cladode face.

croscop (Lake Success, N.Y.) for both the tensile and the compressive regions. Images of areas occupied by libriform fibers, vessels, and those axial and ray parenchyma cells with lignified secondary cell walls in the wood (fibrous zones) were recorded at $\times 30$ with a digital camera (Pixera, Los Gatos, Calif.). The periphery of the fibrous zones was traced using a digitizing tablet and pen, and the traced areas were analyzed using Image ProPlus (Media Cybernetics, Silver Spring, Md.), which was calibrated to $\times 30$ using a stage micrometer.

Biomechanical Analyses

To relate anatomy to junction strength, the elastic modulus (E , Pa = N m^{-2}) was determined for each junction plus its collar. Based on beam theory, flexural stiffness (N m) for a beam supported at one end is E times the second moment of

area of the junction plus the portion of the collar of the upper cladode contacting that of the lower cladode (I , m^4), which describes the bending resistance:

$$\text{flexural stiffness} = EI = \frac{FL^3}{3\delta}, \quad (1)$$

where F (N) is the applied force, L (m) is the length of the cladode, and δ (m) is the deflection of the cladode (Timoshenko and Young 1962; Niklas 1992; Hearn 1997). The E effective for the junction including the collar was determined by dividing the flexural stiffness by I for the elliptical cross section, which was calculated using (Niklas 1992)

$$I = \frac{\pi}{64}a^3b, \quad (2)$$

where a (m) is the axial length in the plane of bending (in-

cluding the collar on the side experiencing compression resulting from bending) and b (m) is the axial length perpendicular to that plane (ignoring the collar).

Statistical Analyses

Descriptive statistics, Student's t -test, and ANOVAs were performed using SigmaStat 2.03 (SPSS, Chicago). Reduced major-axis regressions for log-transformed junction areas and cladode masses were performed as described in Niklas (1994). Data are presented as means \pm 1 SE.

Results

Morphology

Plants of *Nopalea cochenillifera* were approximately half the height of those of *Opuntia ficus-indica*, *Opuntia robusta*, and *Opuntia undulata* (table 1). Cladodes of *N. cochenillifera* were 53%–60% of the length of those of the other three species. Terminal cladodes of *O. ficus-indica* and *O. undulata* were 31% longer than those of *O. robusta*, whereas subterminal cladode length did not differ among the three *Opuntia* species (table 1). Sub-subterminal cladodes of *O. undulata* were 30% longer than those of *O. robusta*, and those of *O. ficus-indica* were intermediate in length. For all four species, cladode length did not differ among the three cladode positions (table 1). Cladodes of *N. cochenillifera* had the smallest masses, averaging 19% of those of the other three species (table 1). Cladodes did not differ in mass among *O. ficus-indica*, *O. robusta*, and *O. undulata* for any of the three cladode positions (table 1). Terminal cladodes differed in mass from subterminal cladodes only for *O. robusta*, for which subterminal cladodes were 60% more massive than terminal cladodes (table 1). For *N. cochenillifera*, sub-subterminal cladodes did not significantly differ in mass from subterminal cladodes. Sub-subterminal cladodes were 52%, 41%, and 71% more massive than terminal cladodes for *O. ficus-indica*, *O. robusta*, and *O. un-*

dulata, respectively (table 1). The cladode angle (α ; fig. 1A) for terminal cladodes of *O. ficus-indica* was greater than those of the other three species, whereas the angle for subterminal cladodes of *O. undulata* was greater than those of the other three species. Sub-subterminal cladodes had the greatest angles for *O. undulata* and *O. ficus-indica*, followed by *O. robusta* and *N. cochenillifera* (table 1). Cladode angles did not differ among the three cladode positions for any of the three species.

The areas of the collar, phloem, wood, and pith increased from terminal to sub-subterminal junctions for all species, except for the collar areas of *O. ficus-indica* and the pith areas for *O. undulata*, which did not change with position (table 2). The collar became less prominent for older junctions; the ratios of the collar area to the junction area (area of phloem, wood, and pith) were 2.04, 1.48, 0.66 for *N. cochenillifera*; 1.33, 0.99, and 0.33 for *O. ficus-indica*; 0.98, 0.49, and 0.38 for *O. robusta*; and 1.33, 0.62, and 0.55 for *O. undulata* for terminal, subterminal, and sub-subterminal junctions, respectively. Phloem and the suberized tissue occupied similar relative cross-sectional area of the junction with age for every species (table 2). The percentage area of the junction occupied by the phloem and suberized tissue averaged 31% for *N. cochenillifera*, 34% for *O. ficus-indica*, 23% for *O. robusta*, and 24% for *O. undulata*. The relative cross-sectional area of wood was similar with junction position for each species, averaging 63% for *N. cochenillifera*, 64% for *O. ficus-indica*, and 75% for *O. robusta* and *O. undulata* (table 2). The relative area of the junction occupied by the pith was <8% for all junctions of all four species.

Junction size did not increase isometrically with increases in the mass of the upper cladodes (fig. 2). Specifically, the scaling exponent was 1.59 ± 0.08 for the log-log relationship of the junction area versus the mass of their upper cladodes for the four species considered together ($r^2 = 0.81$; fig. 2). For the four species considered individually, the scaling exponents were 2.21 ± 0.41 for *N. cochenillifera*, 2.66 ± 0.31 for *O.*

Table 1

Morphological Characteristics of Plants and Cladodes

Characteristic	<i>Nopalea cochenillifera</i>	<i>Opuntia ficus-indica</i>	<i>Opuntia robusta</i>	<i>Opuntia undulata</i>
Plant height (m)	0.87 \pm 0.11 ^A	1.93 \pm 0.16 ^B	1.77 \pm 0.13 ^B	1.90 \pm 0.49 ^B
Cladode length (m):				
Terminal	0.203 \pm 0.006 ^{Aa}	0.410 \pm 0.031 ^{Ba}	0.297 \pm 0.009 ^{Ca}	0.369 \pm 0.010 ^{Ba}
Subterminal	0.181 \pm 0.015 ^{Aa}	0.355 \pm 0.027 ^{Ba}	0.316 \pm 0.011 ^{Ba}	0.345 \pm 0.023 ^{Ba}
Sub-subterminal	0.185 \pm 0.012 ^{Aa}	0.367 \pm 0.017 ^{BCa}	0.310 \pm 0.015 ^{Ba}	0.403 \pm 0.031 ^{Ca}
Cladode mass (kg):				
Terminal	0.218 \pm 0.037 ^{Aa}	1.103 \pm 0.138 ^{Ba}	1.023 \pm 0.058 ^{Ba}	1.126 \pm 0.142 ^{Ba}
Subterminal	0.300 \pm 0.051 ^{Aab}	1.382 \pm 0.129 ^{Ba}	1.641 \pm 0.160 ^{Bb}	1.532 \pm 0.177 ^{Ba}
Sub-subterminal	0.400 \pm 0.055 ^{Ab}	2.096 \pm 0.151 ^{Bb}	2.314 \pm 0.234 ^{Bc}	2.619 \pm 0.336 ^{Bb}
Cladode angle (°):				
Terminal	22 \pm 8 ^{Aa}	51 \pm 22 ^{Ba}	25 \pm 8 ^{Aa}	38 \pm 14 ^{Aa}
Subterminal	46 \pm 17 ^{Aa}	47 \pm 21 ^{Aa}	35 \pm 12 ^{Aa}	60 \pm 10 ^{Ba}
Sub-subterminal	21 \pm 7 ^{Aa}	55 \pm 24 ^{BCa}	33 \pm 11 ^{BAa}	67 \pm 8 ^{Ca}

Note. Plant height, cladode length, cladode mass, and the cladode angle from the vertical (α ; fig. 1A) are means \pm 1 SE ($n = 5$ for *N. cochenillifera*, *O. ficus-indica*, and *O. undulata*; $n = 9$ for *O. robusta*). Values with different uppercase superscript letters within a row are significantly different ($P < 0.05$) after Tukey pairwise multiple comparisons following a one-way ANOVA ($P < 0.05$), as are values with different lowercase superscript letters along a column for a species. Comparisons among species for cladode length and cladode mass were for log-transformed data.

Table 2
Areas (10^{-6} m^2) for the Collars and Tissues of Junctions

Species and position	Collar	Phloem and suberized tissue	Wood	Pith
<i>Nopalea cochenillifera</i> :				
Terminal	110 ± 11 ^A	19 ± 2 ^A	31 ± 3 ^A	3.9 ± 0.9 ^A
Subterminal	174 ± 38 ^{AB}	37 ± 13 ^A	76 ± 23 ^B	4.5 ± 1.0 ^A
Sub-subterminal	248 ± 22 ^B	102 ± 22 ^B	261 ± 81 ^C	14.6 ± 7.1 ^B
<i>Opuntia ficus-indica</i> :				
Terminal	516 ± 84 ^A	114 ± 18 ^A	263 ± 68 ^A	8.4 ± 2.2 ^A
Subterminal	696 ± 66 ^A	260 ± 36 ^A	431 ± 24 ^B	12.5 ± 2.3 ^{AB}
Sub-subterminal	751 ± 98 ^A	825 ± 214 ^B	1451 ± 53 ^C	24.7 ± 6.2 ^B
<i>Opuntia robusta</i> :				
Terminal	484 ± 60 ^A	125 ± 14 ^A	354 ± 29 ^A	16.6 ± 2.0 ^A
Subterminal	628 ± 56 ^{AB}	306 ± 46 ^B	964 ± 245 ^B	17.9 ± 3.0 ^{AB}
Sub-subterminal	835 ± 93 ^B	476 ± 65 ^B	1993 ± 284 ^C	35.9 ± 8.2 ^B
<i>Opuntia undulata</i> :				
Terminal	367 ± 71 ^A	89 ± 10 ^A	175 ± 40 ^A	9.6 ± 1.0 ^A
Subterminal	543 ± 60 ^A	190 ± 39 ^B	674 ± 16 ^B	16.2 ± 2.6 ^A
Sub-subterminal	1460 ± 393 ^B	434 ± 106 ^B	2195 ± 109 ^C	14.9 ± 2.5 ^A

Note. Data are means ± 1 SE ($n = 5$ for *N. cochenillifera*, *O. ficus-indica*, and *O. undulata*; $n = 9$ for *O. robusta*). Values with different superscript letters in a column for a species are significantly different ($P < 0.05$) after Tukey pairwise multiple comparisons following a one-way ANOVA ($P < 0.05$).

ficus-indica, 1.77 ± 0.18 for *O. robusta*, and 2.49 ± 0.33 for *O. undulata*.

Collar and Junction Wood Anatomy

The ratio of the extent of the collar experiencing compressive stresses to the extent experiencing tensile stresses in the field averaged 1.4 for *N. cochenillifera*, 1.3 for *O. ficus-indica*, 1.2 for *O. robusta*, and 1.9 for *O. undulata* (fig. 1B). Collars of terminal junctions for all four species had a single-layered epidermis and a hypodermis consisting of three to five layers of collenchyma cells, both radially and axially. Chlorenchyma made up the innermost portions of the collar. Suberization, indicated by a lack of staining with toluidine blue and red staining with phloroglucinol, of the collar epidermis had begun for virtually all of the terminal junctions observed, and for sub-subterminal junctions, the epidermis was completely suberized and phelloderm development was evident.

The ratio of wood in the region experiencing compressive stresses compared to the region experiencing tensile stresses in the field was >1 (Student's t -test, $P < 0.05$), except for terminal junctions of *O. robusta* and *O. undulata* (fig. 3). This ratio increased from terminal to subterminal junctions, which did not differ from sub-subterminal junctions (one-way ANOVA, $P < 0.05$; fig. 3), except for *O. ficus-indica*. In particular, the compression/tension extent increased 27% from terminal to subterminal and sub-subterminal junctions for *N. cochenillifera*, did not change for *O. ficus-indica*, and increased 37% for *O. robusta* and 178% for *O. undulata*.

Ray widths adjacent to the vascular cambium did not differ between areas experiencing compression and those experiencing tension, except for subterminal junctions of *O. undulata* and sub-subterminal junctions of *N. cochenillifera* and *O. robusta*, all three of which had wider rays in compression areas than in tension areas (table 3). Ray widths in tensile and compressive regions did not change with junction position, except

for *N. cochenillifera*, for which rays in compressive regions of sub-subterminal junctions were 125% wider than those of terminal and subterminal junctions, and *O. undulata*, for which rays in compressive regions of subterminal junctions were 71% wider than those of terminal junctions (table 3). The widths

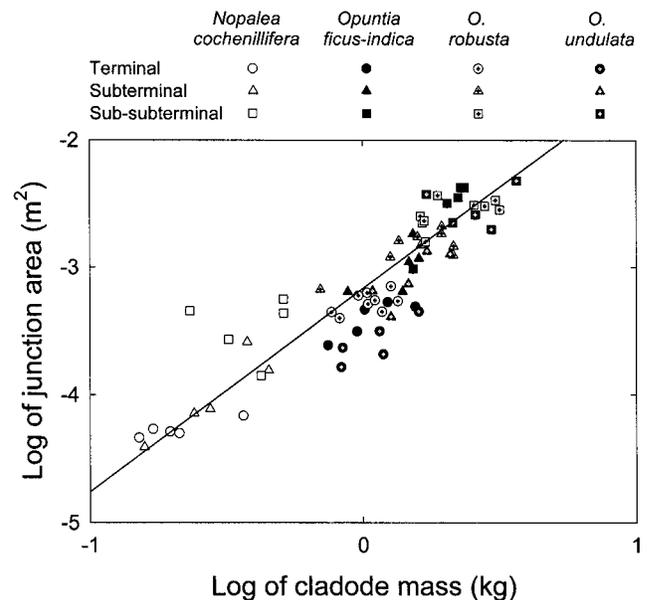


Fig. 2 Log-log relationship between junction area and the mass of the upper cladode of a junction for the three junction positions for all four species. Junction area included the phloem, suberized tissue, wood, and pith (fig. 1B). The equation of the line, $\log(\text{junction area}) = -3.17 + 1.59 \log(\text{upper cladode mass})$, was obtained using a reduced major-axis regression, for which the scaling exponent ($\alpha_{\text{RMA}} = 1.59$) equals the regression coefficient divided by the r value for the least squares regression of the same data ($r^2 = 0.81$).

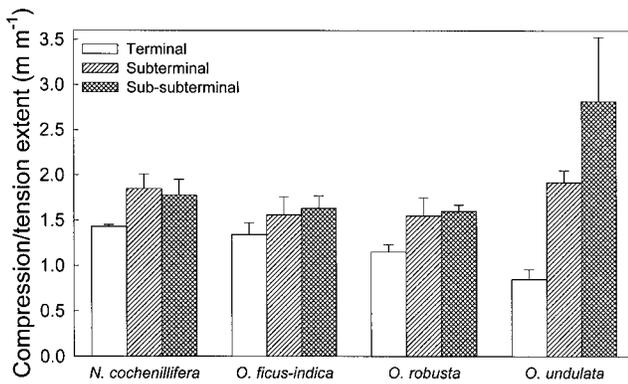


Fig. 3 Ratio of the radial extent of wood in the region experiencing maximum compressive stresses to the radial extent in the region experiencing maximum tensile stresses for the three junction positions of all four species. Data are means \pm 1 SE ($n = 5$ for each junction position for each species).

of axial regions did not differ between areas under compression versus under tension for any of the three junction positions of the four species, except for sub-subterminal junctions of *O. ficus-indica* (table 3). Axial region widths did not change with junction position for *N. cochenillifera* or *O. robusta*. For *O. ficus-indica*, the widths of axial regions increased 63% from terminal to subterminal and sub-subterminal junctions in tensile regions and increased 60% from terminal to subterminal junctions and 128% from subterminal to sub-subterminal junctions in compressive regions (table 3). For *O. undulata*, axial region width increased 150% and 78% from terminal to subterminal and sub-subterminal junctions in tensile regions and compressive regions, respectively (table 3).

Fibrous zones in wood often included lignified axial and ray parenchyma cells and vessels and were present only in sub-terminal and sub-subterminal junctions of *O. ficus-indica*, *O. robusta*, and *O. undulata*. The area of these zones averaged 5.55 ± 2.16 mm² for subterminal junctions and 218 ± 40 mm² for sub-subterminal junctions of *O. ficus-indica*, 0.94 ± 1.20 mm² for subterminal junctions and 6.89 ± 1.38 mm² for sub-subterminal junctions of *O. robusta*, and 1.43 ± 0.58 mm² for subterminal junctions and 15.8 ± 3.8

mm² for sub-subterminal junctions of *O. undulata*. Fibrous zones occurred primarily in the lateral sectors for all three species. The percentages of the total area of fibrous zones in lateral zones of subterminal and sub-subterminal junctions, respectively, were 78% and 66% for *O. ficus-indica*, 77% and 63% for *O. robusta*, and 82% and 100% for *O. undulata*. Fibrous zones were absent from compressive sectors of sub-terminal junctions of *O. robusta* and subterminal and sub-subterminal junctions of *O. undulata*. For *O. ficus-indica*, 10% and 23% of the total area of fibrous zones occurred in compressive sectors of subterminal and sub-subterminal junctions, respectively; for sub-subterminal junctions of *O. robusta*, 9% of the area of fibrous zones occurred in compressive sectors.

Parenchyma cells comprised most of the axial regions and all of the rays in the wood for all four species. All parenchyma cells were unligified for every junction position of *N. cochenillifera*, terminal and subterminal junctions of *O. robusta*, and terminal junctions of *O. ficus-indica* and *O. undulata*. Some parenchyma cells, primarily in axial regions experiencing tensile stresses in the field, developed secondary walls in sub-terminal and sub-subterminal junctions of *O. ficus-indica* (fig. 4A, 4B) and *O. undulata* and in sub-subterminal junctions of *O. robusta*. Lignified axial and ray parenchyma usually occurred in lateral sectors with libriform fibers, often being paratracheal (fig. 4B). Also, zones of very lightly staining parenchyma cells, which appeared to have irregularly thickened walls, occurred in tensile regions in subterminal and sub-subterminal junctions of all four species. These lightly staining parenchyma cells lacked lignin and occurred in the presence (fig. 4B) and absence of libriform fibers.

Most libriform fibers (ca. 80%) appeared gelatinous and occurred primarily near the periphery in the lateral sectors of the junction wood (fig. 4B, 4C). Libriform fibers usually occurred in clusters of at least 10, often completely replacing axial parenchyma and vessels (fig. 4B–4D). Fibrous lignified zones often alternated with zones of lignified or unligified axial parenchyma throughout areas of the junction wood under tension for *O. ficus-indica* and *O. robusta* and the lateral areas (fig. 4B). Lignification of gelatinous libriform fibers occurred primarily in the middle lamellae and the outer part of the cell walls and was greatest at the vertices of the cells (fig.

Table 3

Widths of Rays and Axial Regions Adjacent to the Vascular Cambium for Tensile and Compressive Regions in the Field

Characteristic and junction	<i>Nopalea cochenillifera</i>		<i>Opuntia ficus-indica</i>		<i>Opuntia robusta</i>		<i>Opuntia undulata</i>	
	Tension	Compression	Tension	Compression	Tension	Compression	Tension	Compression
Ray width (mm):								
Terminal	0.17 \pm 0.02 ^{Aa}	0.17 \pm 0.04 ^{Aa}	0.32 \pm 0.15 ^{Aa}	0.65 \pm 0.13 ^{Aa}	0.83 \pm 0.19 ^{Aa}	1.27 \pm 0.36 ^{Aa}	0.46 \pm 0.05 ^{Aa}	0.78 \pm 0.09 ^{Ba}
Subterminal	0.21 \pm 0.02 ^{Aa}	0.23 \pm 0.03 ^{Aa}	0.59 \pm 0.09 ^{Aa}	0.80 \pm 0.20 ^{Aa}	1.28 \pm 0.28 ^{Aa}	1.38 \pm 0.18 ^{Aa}	0.61 \pm 0.05 ^{Aa}	1.33 \pm 0.30 ^{Bb}
Sub-subterminal	0.25 \pm 0.02 ^{Aa}	0.45 \pm 0.06 ^{Bb}	0.63 \pm 0.13 ^{Aa}	0.64 \pm 0.08 ^{Aa}	1.08 \pm 0.11 ^{Aa}	1.63 \pm 0.08 ^{Ba}	0.58 \pm 0.10 ^{Aa}	0.99 \pm 0.30 ^{Ab}
Axial region width (mm):								
Terminal	0.15 \pm 0.03 ^{Aa}	0.14 \pm 0.02 ^{Aa}	0.23 \pm 0.04 ^{Aa}	0.20 \pm 0.03 ^{Aa}	0.16 \pm 0.03 ^{Aa}	0.20 \pm 0.04 ^{Aa}	0.13 \pm 0.01 ^{Aa}	0.16 \pm 0.05 ^{Aa}
Subterminal	0.17 \pm 0.02 ^{Aa}	0.16 \pm 0.02 ^{Aa}	0.37 \pm 0.07 ^{Ab}	0.32 \pm 0.03 ^{Ab}	0.23 \pm 0.06 ^{Aa}	0.23 \pm 0.04 ^{Aa}	0.29 \pm 0.04 ^{Ab}	0.27 \pm 0.05 ^{Ab}
Sub-subterminal	0.16 \pm 0.02 ^{Aa}	0.16 \pm 0.02 ^{Aa}	0.38 \pm 0.05 ^{Ab}	0.73 \pm 0.04 ^{Bc}	0.30 \pm 0.03 ^{Aa}	0.26 \pm 0.04 ^{Aa}	0.36 \pm 0.04 ^{Ab}	0.30 \pm 0.04 ^{Ab}

Note. Data are means \pm 1 SE ($n = 4$ for each junction position). For each species, values with different uppercase superscript letters within a row are significantly different ($P < 0.05$) after Student's *t*-test. For rays and axial regions, values with different lowercase superscript letters within a column are significantly different ($P < 0.05$) after Tukey pairwise multiple comparisons following a one-way ANOVA ($P < 0.05$).

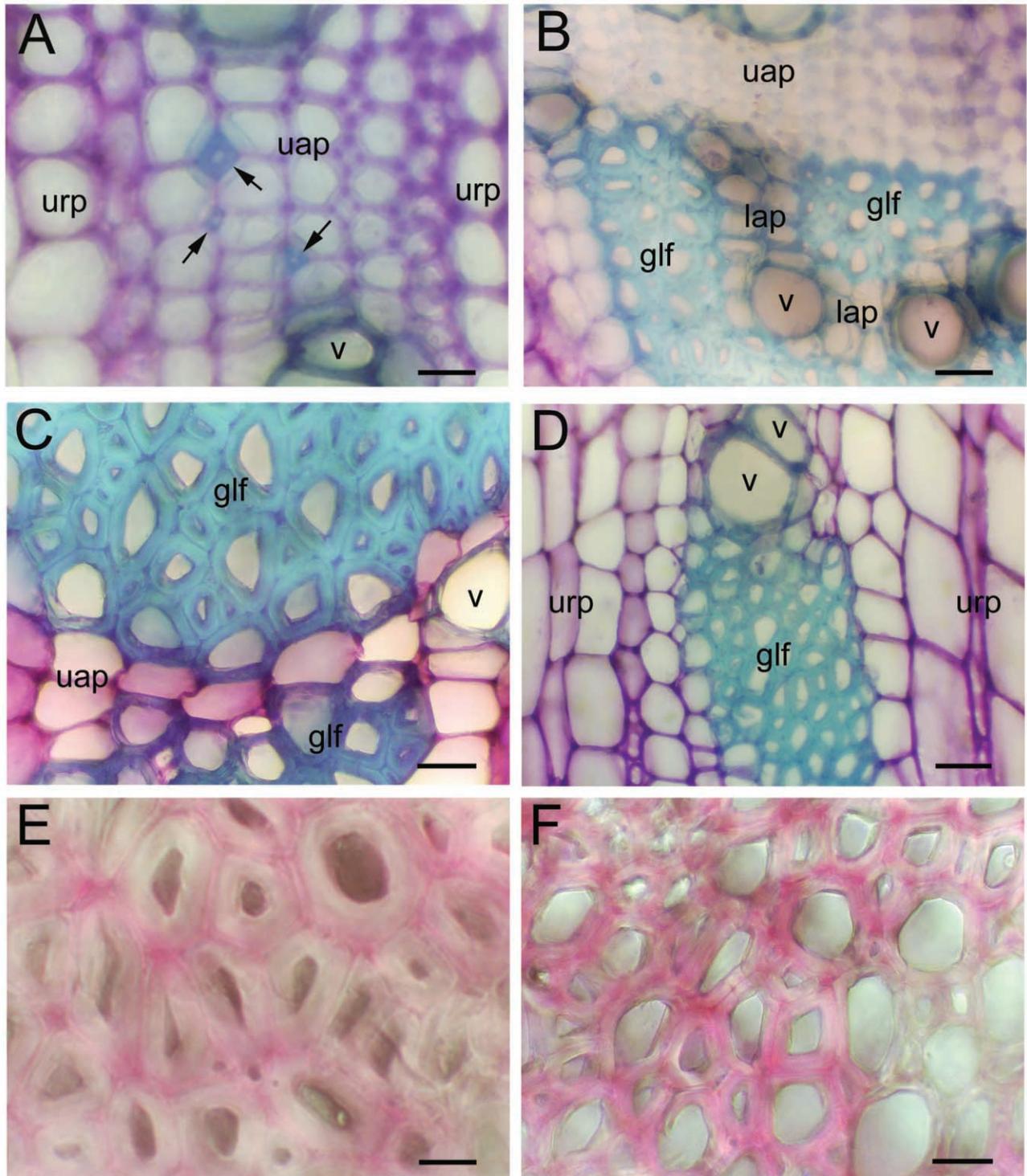


Fig. 4 Photomicrographs of cross sections for reaction wood in sub-subterminal cladode junctions. *A*, Tension region of *Opuntia ficus-indica* stained with toluidine blue showing unlignified axial parenchyma with secondary walls (*uap*), lignification of the vertices of axial parenchyma (arrows), unlignified ray parenchyma (*urp*), and vessels (*v*) (bar = 20 μm). *B*, Tension region of *O. ficus-indica* with lightly staining axial parenchyma radially distal to gelatinous libriform fibers (*glf*), lignified axial parenchyma (*lap*), and vessels (bar = 40 μm). *C*, Tension region of *Opuntia undulata* with gelatinous libriform fibers (bar = 20 μm). *D*, Compression region of *Opuntia robusta* with gelatinous libriform fibers and unlignified parenchyma and vessels (bar = 40 μm). *E*, Gelatinous libriform fibers of *O. undulata* stained with phloroglucinol showing lignification in the middle lamellae and oldest layers of cell walls (bar = 10 μm). *F*, Libriform fibers of *O. undulata* varying in the lignification of their cell walls (bar = 20 μm).

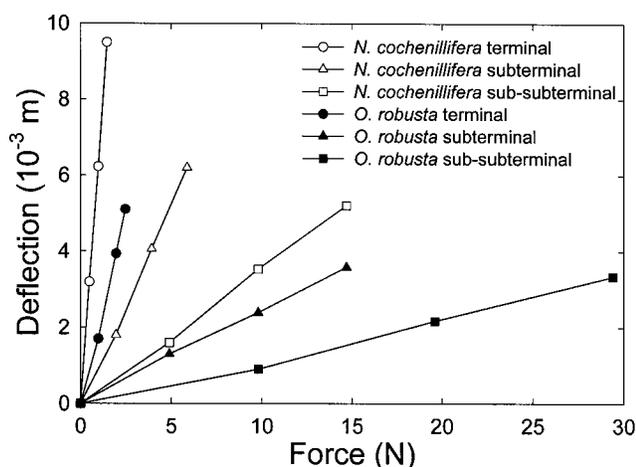


Fig. 5 Forces and their resulting deflections for representatives of each junction position for *Nopalea cochenillifera* and *Opuntia robusta*. Forces were applied parallel to the cladode face toward the region experiencing maximal compressive stresses in the field.

4E). The G-layer was thick, stained lightly with toluidine blue, and usually did not stain at all with phloroglucinol, indicating a lack of lignin (fig. 4B–4E). The walls of fibers located on the periphery of clusters stained darker with toluidine blue (fig. 4C) and often stained positively for lignin in their secondary walls. In rarer cases, lignification of cell walls of fibers was highly variable throughout the cluster (fig. 4F).

Biomechanics

Cladode deflection increased linearly with increasing force over the range of forces used and decreased from terminal to

subterminal to sub-subterminal cladodes for a given force (fig. 5). Deflection for a given force did not differ for bending parallel compared with perpendicular to the cladode face for the three cladode positions for the four species (table 4). The deflection per force for terminal cladodes for bending parallel or perpendicular to the cladode face averaged 4.2, 7.0, 6.5, and 12.0 times greater than that for subterminal cladodes of *N. cochenillifera*, *O. ficus-indica*, *O. robusta*, and *O. undulata*, respectively (table 4). Deflection per force for subterminal cladodes averaged 4.0, 10.0, 2.4, and 7.5 times greater than that for sub-subterminal cladodes for the four species (table 4).

Junction flexural stiffness, which is inversely proportional to the cladode deflection per applied force, did not differ for bending parallel versus perpendicular to the cladode face for any of the three junction positions for the four species (table 4). Junction flexural stiffness increased from terminal to subterminal to sub-subterminal junctions. Specifically, the flexural stiffness of subterminal junctions for bending parallel or perpendicular to the cladode face averaged 5.8, 5.2, 4.4, and 11.4 times greater than the flexural stiffness of terminal junctions for *N. cochenillifera*, *O. ficus-indica*, *O. robusta*, and *O. undulata*, respectively. The flexural stiffness of sub-subterminal junctions averaged 3.7, 8.7, 4.2, and 7.1 times greater than that for subterminal junctions for the four species (table 4).

The effective elastic modulus (E) of the junctions, including resistance provided by the collar, did not differ for bending parallel or perpendicular to the cladode face for any of the three junction positions for the four species (table 4). Of the four species, *O. robusta* had the lowest effective E for all three junction positions, and *N. cochenillifera* had the highest for terminal and subterminal junctions (one-way ANOVA, $P < 0.05$). Values of E for terminal and subterminal junctions were intermediate for *O. ficus-indica* and *O. undulata*. The values

Table 4

Cladode Deflection per Applied Force, Junction Flexural Stiffness (EI), and Effective Elastic Moduli (E) of Junctions for Bending of Cladode Junctions Parallel to the Cladode Face in the Direction of Maximum Compressive Stresses in the Junction in the Field (Fig. 1C) or Perpendicular to the Cladode Face (Fig. 1D)

Species and position	Deflection/force (mm N ⁻¹)		Flexural stiffness (N m ²)		Elastic modulus (MPa)	
	Parallel	Perpendicular	Parallel	Perpendicular	Parallel	Perpendicular
<i>Nopalea cochenillifera</i> :						
Terminal	5.1 ± 1.2 ^{Aa}	5.4 ± 1.2 ^{Aa}	0.47 ± 0.06 ^{Aa}	0.44 ± 0.04 ^{Aa}	858 ± 77 ^{Aa}	679 ± 56 ^{Aa}
Subterminal	1.2 ± 0.2 ^{Ab}	1.3 ± 0.2 ^{Ab}	2.7 ± 0.8 ^{Ab}	2.6 ± 0.8 ^{Ab}	725 ± 91 ^{Aa}	731 ± 142 ^{Aa}
Sub-subterminal	0.29 ± 0.08 ^{Ac}	0.32 ± 0.10 ^{Ac}	10 ± 3 ^{Ac}	9.5 ± 3.0 ^{Ac}	631 ± 118 ^{Aa}	635 ± 43 ^{Aa}
<i>Opuntia ficus-indica</i> :						
Terminal	1.9 ± 0.2 ^{Aa}	3.0 ± 0.6 ^{Aa}	13 ± 4 ^{Aa}	7.4 ± 2.0 ^{Aa}	431 ± 55 ^{Aa}	354 ± 55 ^{Aa}
Subterminal	0.24 ± 0.06 ^{Ab}	0.45 ± 0.13 ^{Ab}	70 ± 18 ^{Ab}	44 ± 16 ^{Ab}	459 ± 49 ^{Aa}	332 ± 35 ^{Aa}
Sub-subterminal	0.03 ± 0.01 ^{Ac}	0.04 ± 0.01 ^{Ac}	504 ± 28 ^{Ac}	447 ± 43 ^{Ac}	495 ± 75 ^{Aa}	438 ± 32 ^{Aa}
<i>Opuntia robusta</i> :						
Terminal	1.5 ± 0.21 ^{Aa}	1.9 ± 0.3 ^{Aa}	6.9 ± 0.7 ^{Aa}	5.8 ± 0.9 ^{Aa}	210 ± 20 ^{Aa}	176 ± 12 ^{Aa}
Subterminal	0.24 ± 0.06 ^{Ab}	0.28 ± 0.06 ^{Ab}	35 ± 5 ^{Ab}	22 ± 4 ^{Ab}	173 ± 10 ^{Aa}	160 ± 21 ^{Aa}
Sub-subterminal	0.09 ± 0.02 ^{Ac}	0.13 ± 0.03 ^{Ac}	124 ± 15 ^{Ac}	105 ± 13 ^{Ac}	193 ± 9 ^{Aa}	201 ± 16 ^{Aa}
<i>Opuntia undulata</i> :						
Terminal	5.2 ± 1.0 ^{Aa}	5.5 ± 0.6 ^{Aa}	4.04 ± 1.04 ^{Aa}	3.47 ± 0.40 ^{Aa}	346 ± 66 ^{Aa}	345 ± 71 ^{Aa}
Subterminal	0.41 ± 0.18 ^{Ab}	0.48 ± 0.19 ^{Ab}	44.6 ± 11.7 ^{Ab}	40.5 ± 14.8 ^{Ab}	464 ± 55 ^{Aa}	403 ± 57 ^{Aa}
Sub-subterminal	0.05 ± 0.01 ^{Ac}	0.07 ± 0.01 ^{Ac}	348 ± 49 ^{Ac}	258 ± 44 ^{Ac}	481 ± 81 ^{Aa}	344 ± 71 ^{Aa}

Note. Data are means ± 1 SE ($n = 5$ for *N. cochenillifera*, *O. ficus-indica*, and *O. undulata*; $n = 9$ for *O. robusta*). Values with different uppercase superscript letters within a row are significantly different ($P < 0.05$) after Student's t -test. Values with different lowercase superscript letters in a column for a species are significantly different for log-transformed data after Tukey pairwise multiple comparisons ($P < 0.05$) following a one-way ANOVA ($P < 0.05$).

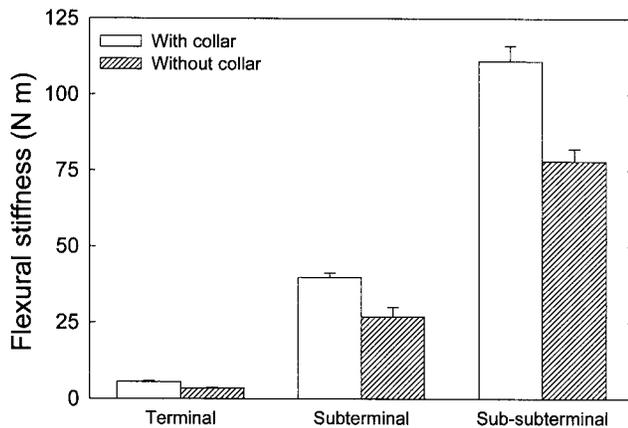


Fig. 6 Effect of collar removal on the flexural stiffness for three junction positions of *Opuntia robusta*. Data are means \pm 1 SE ($n = 4$ for each junction position).

of E for sub-subterminal junctions did not differ between *N. cochenillifera*, *O. ficus-indica*, and *O. undulata* (one-way ANOVA, $P > 0.05$).

Removal of the collar from the upper cladode of a junction of *O. robusta* decreased flexural stiffness (fig. 6). In particular, mean flexural stiffnesses for terminal, subterminal, and sub-subterminal junctions decreased 38%, 33%, and 30%, respectively, after collars were removed (Student's t -test, $P < 0.05$). Hence, increases in flexural stiffness from terminal to subterminal to sub-subterminal junctions were similar for junctions with collars and after collar removal (fig. 6). Specifically, flexural stiffnesses for subterminal junctions were 7.2 and 8.0 times greater than for those of terminal junctions with collars and without collars, respectively. Flexural stiffnesses for sub-subterminal junctions were 2.8 and 2.9 times greater than those of subterminal junctions for the two conditions, respectively.

Discussion

A major trait of reaction wood, eccentricity of the pith (Fahn 1990), was evident in terminal, subterminal, and sub-subterminal cladode junctions of *Nopalea cochenillifera* and *Opuntia ficus-indica* as well as in the subterminal and sub-subterminal junctions of *Opuntia robusta* and *Opuntia undulata*. Pith eccentricity resulted from a greater wood extent in the compressive regions of junctions than in the tensile regions, in contrast to the reaction wood of many other dicotyledons, which typically have a greater wood extent in tensile than in compressive regions (Fahn 1990; Hejnowicz 1997). Wood in the compressive regions of these arborescent platyopuntias consisted primarily of thin-walled parenchyma. Because parenchyma resists compressive stresses better than tensile stresses (Niklas 1992), greater wood growth in compressive regions compared with other regions may allow junctions to resist loads without the energy costs involved in lignification of cell walls. Increasing the extent of wood in compressive compared with tensile regions from terminal junctions to the two older positions for *N. cochenillifera*, *O. robusta*, and *O.*

undulata may be a direct response to the load associated with the addition of new cladodes to a branch. Having a collar twice as large for the compressive compared with the tensile side may compensate for the lack of eccentric pith in terminal junctions of *O. undulata*. Because *O. robusta* had the largest terminal junctions, asymmetrical wood deposition may not be necessary for it.

Another trait for reaction wood in dicotyledons is the presence of gelatinous fibers (Fisher and Stevenson 1981; Hejnowicz 1997), which also occur in older cladode junctions of platyopuntias (Bobich and Nobel 2001a). When present, gelatinous fibers are generally more frequent on the upper sides of stems in dicotyledons but may be present on the lower sides near the pith or may even form complete rings within a stem (Fisher and Stevenson 1981; Fahn 1990; Carlquist 2000). For *O. ficus-indica*, *O. robusta*, and *O. undulata*, fibers were libriform, mostly gelatinous, similar to wood of certain *Fouquieria* species (Carlquist 2000), and occurred in greater numbers in lateral regions than in tensile and compressive regions. Such a location may not function in decreasing branch angle from the vertical, which is the case for many woody dicotyledons with gelatinous fibers in the upper regions of their stems (Fisher and Stevenson 1981; Mueller 1988; Wilson 1998). If gelatinous fibers in these platyopuntias contract as they do for many tree stems (Fournier et al. 1994) and aerial roots of tropical species (Fisher 1982), the gelatinous fibers may prevent branches from swaying as a result of wind directed toward the flat sides of the cladodes.

Subterminal and sub-subterminal junctions of *O. ficus-indica* had prominent normal and gelatinous libriform fibers, indicating they may have experienced greater internal stresses resulting from bending than those of *O. robusta* and *O. undulata* (Fisher and Stevenson 1981) and also had a high percentage of the fibrous zones in the compressive regions (10% and 23% for subterminal and sub-subterminal junctions, respectively). Because *O. ficus-indica* can have the most fruits of the four species, up to 20 fruits per terminal cladode with each fruit weighing up to 0.15 kg at maturity (Barbera et al. 1995; E. G. Bobich and P. S. Nobel, personal observations), the gelatinous fibers in the compressive regions of the stem may be a response to internal stresses caused by large static loads. Also, the prominence of fibers in the compressive regions may explain why pith eccentricity did not increase from terminal to subterminal and sub-subterminal junctions of this species. The lack of gelatinous fibers in any of the junctions of *N. cochenillifera* indicates that the mass of its cladodes was not great enough to create internal stresses necessary for fiber formation. This is similar to the Fouquieriaceae, for which reaction wood is extremely common but whose species with relatively light branches completely lack gelatinous fibers (Carlquist 2000).

Other traits of reaction wood are ray dilation and a reduction in the lignification of parenchyma in tensile regions (Fisher and Stevenson 1981; Fisher and Mueller 1983). For subterminal junctions of *O. undulata* as well as for sub-subterminal junctions of *N. cochenillifera* and *O. robusta*, rays were larger at the vascular cambium in compressive regions than in tensile regions. In nonsucculent woods, rays reduce shear between growth rings and provide radial reinforcement (Matthack and Bethge 1998). It is unlikely that the rays of the investigated

platyopuntia junctions perform similar functions because these rays are unligified and the individual cells can more easily experience shear. Zones of very lightly staining parenchyma occurred within the axial regions for the areas under tension for junctions of all four species. The irregular thickening and the light staining with toluidine blue of the walls indicate that these cells may have less cellulose than typical parenchyma cells and may contain larger amounts of pectin or hemicellulose. Also, the darker-staining parenchyma with unligified secondary walls in the tension regions may be analogous to similar cells in wood regions of shrubby and low-growing platyopuntias where fibers are absent (Gibson 1978).

Cladode deflection per applied force for bending parallel to the cladode face in the direction of compressive stresses in the field did not differ from bending perpendicular to the cladode face for the three junction positions of any of the four species. However, cladode deflection per applied force decreased from terminal to subterminal to sub-subterminal junctions for all four species, which was reflected by increases in flexural stiffness with junction age. The increases in flexural stiffness reflected increases in the junction cross-sectional area, which was primarily a result of increases in wood cross-sectional area (Bobich and Nobel 2001a, 2001b) and, to a lesser extent, by the accumulation of secondary phloem and minor increases in pith area (probably resulting from cell division). Increases in wood cross-sectional area also contribute greatly to increases in flexural stiffness with stem length for columnar cacti in the Sonoran Desert (Molina-Freaner et al. 1998). As evidenced by the high scaling exponents with cladode mass, the increases in junction cross-sectional area were especially large for *O. ficus-indica* and *O. undulata*, for which flexural stiffness increased an average of sevenfold and ninefold, respectively, from terminal to subterminal and from subterminal to sub-subterminal junctions. *Opuntia ficus-indica* had the greatest values for junction flexural stiffness, apparently due to its cellular anatomy, whereas *N. cochenillifera* had the smallest values for junction flexural stiffness and the smallest junction cross-sectional areas.

Collar removal resulted in a 34% decrease in flexural stiffness for the three junction positions of *O. robusta*. Because tensile and compressive stresses increase toward the periphery of stems (Niklas 1992), the location of collars relative to junctions increased their importance in resisting compressive forces. The epidermis and the collenchymatous hypodermis stiffen collars (and other regions of cactus stems; Gibson and Nobel 1986), allowing them to resist forces greater than if they consisted solely of parenchyma. Although the epidermis may become stiffer as it becomes more suberized in time (Gibson and Nobel 1986), the contribution of collars to the flexural stiffness of junction regions will probably decrease as junctions age due to the accumulation of wood, which increases junction cross-sectional area.

The elastic modulus (E) for stems of columnar cacti tends to increase with stem length (Molina-Freaner et al. 1998) and generally increases from the apex to the middle of stems for *Pachycereus pringlei* (Niklas et al. 1999). The effective E for the three most terminal junction regions of *N. cochenillifera*, *O. ficus-indica*, *O. robusta*, and *O. undulata* did not significantly differ, even with differences in cellular anatomy, most notably in the presence of fibers in subterminal and sub-

subterminal junctions for the three species with the largest cladodes. Actually, the fibrous zones accounted for <1% of the cross-sectional area for subterminal junctions of *O. ficus-indica* and subterminal and sub-subterminal junctions of *O. robusta* and *O. undulata*; they accounted for only 9% of the cross-sectional area of sub-subterminal junctions of *O. ficus-indica*. Although additional fibers and increased lignification can disproportionately contribute to the E of stems (Tomlinson 1987; Niklas and Buchman 1994; Molina-Freaner et al. 1998), the small percentage of fibers and lignified parenchyma cells may contribute little to junction stiffness compared to the large amount of unligified axial and ray parenchyma cells in the junctions. However, E should increase for junctions older than sub-subterminal junctions because wood of arborescent and shrubby platyopuntias tends to have more libriform fibers and more lignified axial and ray parenchyma as the stems become older (Gibson 1978).

The junctions of all four species had an effective E over 100 times greater than that of a tissue composed solely of parenchyma but less than that of stem tissues of *Carnegiea gigantea*, which has more lignification in its wood (Niklas and Buchman 1994). The value of E of the junction tissues is probably greater than that of tissues consisting solely of parenchyma resulting from the presence of vessels throughout the xylem, the epidermis and hypodermis of the collar, and the organization of axial and ray cells within the wood because these cells and tissues can all stiffen stems (Carlquist 1975; Niklas 1992). Differences in the effective E for junctions plus the collar among the four species considered may be attributable to the ratio of axial cells to ray cells in the wood of each species because axial cells develop from fusiform initials, are smaller in diameter (Gibson 1978), and, consequently, have more contact between cell walls to prevent shearing and more cell wall area per cross-sectional area than do ray cells (Niklas 1988, 1992). The ratios of ray width to axial width for terminal, subterminal, and sub-subterminal junctions were 1.2, 1.3, and 2.2, respectively, for *N. cochenillifera*; 2.3, 2.0, and 1.3 for *O. ficus-indica*; 5.8, 5.8, and 5.0 for *O. robusta*; and 3.0, 3.5, and 2.5 for *O. undulata*. Thus, the junction regions with the greatest effective E —terminal, subterminal, and sub-subterminal junctions of *N. cochenillifera* and subterminal junctions of *O. ficus-indica* and *O. undulata*—had relatively low ratios of ray to axial region width compared with junction regions of *O. robusta*, which had the largest ratios of ray to axial region width and the lowest effective E . Other differences among species, such as cell wall thickness for cells with secondary cell walls (Gibson 1973, 1978; Bobich and Nobel 2001a, 2001b), probably also affect E .

In summary, cladode junctions of arborescent platyopuntias have reaction wood typified by pith eccentricity due to greater wood accumulation in the compressive versus tensile regions and the presence of gelatinous fibers in subterminal and sub-subterminal junctions of species with large cladodes. The hypothesis that the gelatinous fibers would be located in the tensile regions of junctions to counteract bending because of static loading, which is generally the case for dicotyledons (Fisher and Stevenson 1981; Fahn 1990), appears to be incorrect because gelatinous fibers were most frequent in the lateral regions. These fibers may help prevent branch lateral movement caused by wind. Junction flexural stiffness increased

from terminal to subterminal to sub-subterminal junctions for all four species, although these changes were primarily a result of increases in junction cross-sectional area caused by additional secondary phloem and wood, not to changes in the *E* resulting from changes in the cellular anatomy. As hypothesized, the contribution of the collar to resisting bending forces was substantial, accounting for about one-third of the flexural stiffness of the junction region. Thus, although the three youngest junctions of a branch have several anatomical dif-

ferences, the biomechanics due to bending forces are primarily affected by the junction cross-sectional area and the resistance provided by the collar.

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