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Xylem vascular anatomy and water transport of *Salicornia europaea*

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Abstract

The xylem anatomy, changes in vessel member diameter at stem nodes and branch junctions, and effects of these changes on water flow rates and water potential in greenhouse and field grown *Salicornia europaea* L. (Chenopodiaceae) have been investigated. There was a two-fold decrease in vessel diameter at branch junctions and stem nodes. In greenhouse grown plants, this decrease resulted in a 1000-fold decrease in water flow rates, and a four- to eight-fold increase in resistance to water flow across branch junctions and stem nodes relative to within-internode flow rates. However, in field grown plants, there were no differences in water flow across branch junctions and stem nodes compared with water flow within internodes. Water potentials in field plants were 3–15 times lower than in greenhouse plants. Under field conditions, hypersalinity is probably the key determinant of *Salicornia* water relations. Localized reductions in vessel member diameter in *Salicornia* appear to result from developmental changes in vasculature attending axillary bud growth. Reductions in *Salicornia* vessel diameter, therefore, may not be hydraulically functional adaptations per se. Rather, they may reflect a consequence of developmental branching.

Introduction

The hydraulic architecture of plants, including its role in maintaining continuous water transport through the plant, has received much attention from anatomists, physiologists, morphologists, and ecologists (e.g. Zimmermann, 1973, 1978a,b, 1983; Larson and Isebrands, 1978; Kramer, 1983; Tomlinson, 1983, 1987; Zimmermann and Sperry, 1983; Ewers and Zimmermann, 1984a,b; Ewers, 1985; Gibson et al., 1985; Sperry, 1986). For water to flow from roots to leaves, the water potential in the xylem must decrease acropetally. During periods of water stress, the water potential in the xylem falls rapidly and the water column in the xylem may cavitate, resulting in an air

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embolism that stops water flow (Tomlinson, 1983; Zimmermann, 1983; Zimmermann and Sperry, 1983).

Studies of the xylem anatomy of palms and dicotyledonous trees have revealed the presence of constrictions in conducting tracheary elements located at the anatomical junction between branch and leaf, and between trunk and branch. Xylem water potential decreases sharply across these constrictions, and they have been hypothesized to be adaptive structures that restrict air embolisms to peripheral (expendable) organs so that continuous water flow in the main stem is maintained (Zimmermann, 1983; Zimmermann and Sperry, 1983; Tyree et al., 1983; Ewers and Zimmermann, 1984a,b). Examinations by these authors of the hydraulic architecture and water relations of various tree species under stressful conditions have supported this hypothesis.

Tomlinson (1983) hypothesized that hydraulic constrictions would have evolved very early in the history of land plants, and Niklas and Banks (1985) found constrictions in the primary xylem of the Emsian trimerophyte *Psilophyton dawsonii* Banks. Studies of vessel-less ferns, however, have not revealed abrupt xylem water potential decreases from stipe to rachis, and Gibson et al. (1985) stated that if constrictions are present, they have only minor effects on water flow in pteridophytes. Thus, while constrictions may be functionally adaptive, their presence does not indicate a priori selection for hydraulic architecture, but may simply reflect a developmental consequence of unequal branching.

Ferns, palms, conifers, and angiosperm trees and herbs are subject to drought stress and xylem cavitation (e.g. Milburn and McLaughlin, 1974). The majority of research on hydraulic architecture has focused on ferns, palms, conifers, and dicotyledonous trees; relatively little is known about hydraulic architecture and its effect on water relations in herbs. Here, the hydraulic architecture and its effects on water relations in the succulent annual, *Salicornia europaea* L. (Chenopodiaceae) are described.

Salicornia, like other halophytes, inhabits salt marshes, salt pans, and other hypersaline environments (e.g. Ellison, 1987). Previous studies of water relations of halophytes have shown that under normal growing conditions, these plants exhibit some of the lowest water potentials measured (Scholander, 1968; Waisel, 1972; Hadač and Hadačová, 1974; Kuramoto and Brest, 1979; Antlfinger, 1981; Kramer, 1983; Drake and Gallagher, 1984; Salzman and Parker, 1985; Stumpf et al., 1986; Alpert, 1990). In halophytes, very low negative pressures in xylem (down to -4.5 MPa) are needed in order to overcome the osmotic pressure of seawater (e.g. Waisel, 1972; Tomlinson, 1986).

By studying the xylem anatomy and water relations of *Salicornia*, we are examining an extreme. We would expect that, if selection favored the development of structures that maintain continuous flow in stems at the expense of peripheral organs, such structures would be evident in plants that have evolved in and are restricted to hypersaline environments. That is, although patterns illustrated by *Salicornia* may not be general, they may represent an end-point along a continuum of evolutionary trends in hydraulic architecture and responses to chronic water stress.

Materials and methods

Study species

Salicornia europaea is an annual, succulent halophyte common to salt marshes and beaches in eastern North America (Ellison, 1987; Ellison and Niklas, 1988). The stem consists of a series of internodes, each about 1 cm long. Plants are often profusely branched, and may reach 50 cm in height. Details on the ecology of *Salicornia* are given in Ellison (1987).

Although the basic anatomy of *Salicornia* and related chenopods has been described by De Fraine (1912), Fahn and Arzee (1959), and Anderson (1974), a complete description of the anatomy of *Salicornia* is lacking. *Salicornia* plants appear leafless; all photosynthesis occurs in the chlorenchyma surrounding the stem. The ontogenetic origin of *Salicornia*'s photosynthetic tissue has been debated for over a century. The fleshy 'cortex' has been considered to be of foliar origin through reduction (e.g. Duval-Jouve, 1868; De Fraine, 1912) or through fusion followed by adnation (e.g. James and Kyhos, 1961). Fahn (1963) and Fahn and Arzee (1959) consider the photosynthetic tissue to be the true stem cortex, and conclude that *Salicornia* is truly leafless. This controversy has not yet been satisfactorily resolved (reviewed by Scott, 1977). If leaves, or leaf homologues are present, they are sufficiently reduced to lack vasculature (De Fraine, 1912; Fahn and Arzee, 1959). However, the morphological and anatomical interpretation of the origin of the fleshy cortex of *Salicornia* is irrelevant in the context of this study. The identification and function of these anatomical features are independent of the organographic identity of hydraulically linked structures.

Xylem anatomy

Twenty adult *Salicornia* plants were collected randomly in August 1986 from a large population growing in a 200 m^2 area between +1.0 and +1.2 m mean tidal height at Brown University's Haffenreffer Preserve, Bristol, RI. Although *Salicornia europaea* was the dominant dicotyledonous species in this area, *S. virginica* L., *Suaeda maritima* (L.) Dum., *Atriplex triangularis* Willd., and *Limonium nashii* Small., were also present. Collected plants were placed immediately into a solution containing formalin, acetic acid, and 95% ethanol (FAA solution) for fixation. Standard paraffin techniques (Berlyn and Miksche, 1976) were used to prepare transverse sections (10 μm thick) through small segments (1–2 cm) of the plants consisting of two nodes and one internode. Sections were mounted on slides, stained with safranin and fast green (Fahn and Arzee, 1959; Berlyn and Miksche, 1976), and photographed. Anatomical details on photographs were digitized into the memory of an IBM PC-XT computer using a GTCO digipad and 16 button cursor. Xylem diameters and paths of vessels through the stem segment were calculated using the computer program SECTION (Niklas and Boyd, 1987).

Water potential measurements

We used a Scholander-type pressure bomb (Scholander et al., 1965) to measure the xylem water potential of field and greenhouse grown *Salicornia* plants. Water potential measurements made with pressure bombs are known to be well correlated with stem psychrometer measurements, although the two often give values differing by up to − 1.0 MPa (reviewed by Hardegree, 1989). So that our measurements could be reliably compared with previous work on hydraulic architecture and water relations (in general and for related chenopods), we used the pressure bomb in all our studies. We were unable to obtain transpiration measurements for comparative purposes; the apparent 'leaflessness' of *Salicornia* was not compatible with available PLC broad leaf chambers on a LCA-2 IRGA (Analytical Development Corporation); alternative methods described by Pearcy et al. (1989), while adequate for flat leaves, are not practicable for *Salicornia.*

To estimate field soil water potential, water potentials of unstressed plants growing at Brown University's Haffenreffer Preserve were measured on 5 September 1987 before dawn as the plants were uncovered by the receding tide. Substrate salinity at Haffenreffer was approximately 35‰. Water potential measurements of stressed plants in the field were taken between 12:00 and 14:00 h under full sun on 5 September 1987. Xylem water potential was measured on main stems and on primary branches. We measured both the water potential within an internode as well as the pressure needed to force water across a node. To measure water potential within an internode, the cut end of the plant was inserted through the rubber gasket of the pressure bomb such that the node above the cut was well inside the pressure chamber. To measure the (expected) increase in resistance to flow across a node, the node above the cut was positioned above the rubber gasket, outside of the pressure chamber. In both cases, the length of stem segment outside the pressure chamber was kept constant at 5 mm. Because of possible resistance to water flow at points of reduction in vessel diameter (such as nodes) that could affect water potential measurements, we pressurized samples at a relatively slow rate (less than 1 MPa min^{-1}).

Plants were also raised in the greenhouse under less saline conditions to determine xylem water potentials in less-stressed plants. *Salicornia* seedlings were collected together with local soil from Rumstick Cove, Barrington, RI, and transported to Cornell University's greenhouses in March 1987. The seedlings were placed in plastic flats (60 cm × 30 cm × 6 cm) in an unheated greenhouse. No supplemental light or fertilizer was used. These plants were watered with fresh water; soil salinity was maintained at 10‰ by adding Instant Ocean artificial seawater when necessary. Soil salinity concentrations between 10 and 20‰ are considered optimal for growth of many *Salicornia* species (Webb and Burley, 1965; Webb, 1966; Tiku, 1976; Abdulrahman and Williams, 1981), and plants growing in lower or higher salinities often show reductions in growth rate and/or size. Xylem water potentials of the greenhouse grown plants were measured at the same time, and in the same way, as the field grown plants.

Fluid flow rate through xylem

We measured the flow rate of liquid through the stem (hydraulic conductivity) using the method of Zimmermann (1978a). Measured, trimmed stem sections consisting of an internode (either with or without the node directly above the internode) were suspended from the end of a 2 ml pipette filled with a 10% KCl solution. Sections with nodes removed were used to assess flow rates in sections where reductions in vessel diameter did not occur, while sections with intact nodes were used to assess flow rates across areas where vessel diameter reduction occurred. The flow rate was measured at 30 s intervals at a pressure gradient adjusted for the length of the stem segment: 10.13 kPa $m^{-1} \times [(h+L)/L]$, where h is the average height of the water column above the specimen and L is the length of the stem segment (Zimmermann, 1978a; M. Tyree, personal communication, 1990). Flow rate measurements were made only for greenhouse grown plants. We also recorded the fresh tissue weight of the plant above the stem section used in these measurements to determine if flow rate through a section was related to the amount of plant tissue supplied through that section (Zimmermann, 1978a, 1983; Ewers, 1985).

Results

Xylem anatomy

Internodal and nodal anatomy is reconstructed in Figs. 1–2, based on serial sections through six shoots bearing lateral branches. The reconstruction shows three nodes, labelled A–C, acropetally. In transverse section, six primary vascular strands are seen below each node. Vascular traces ascending the two internodes of each specimen are labelled 1–4; traces diverging into nodes are labelled a–f. At Node A, six traces ascend through the main shoot (1–4, c and d) while two traces (a and b) diverge into Node A. These two traces are not

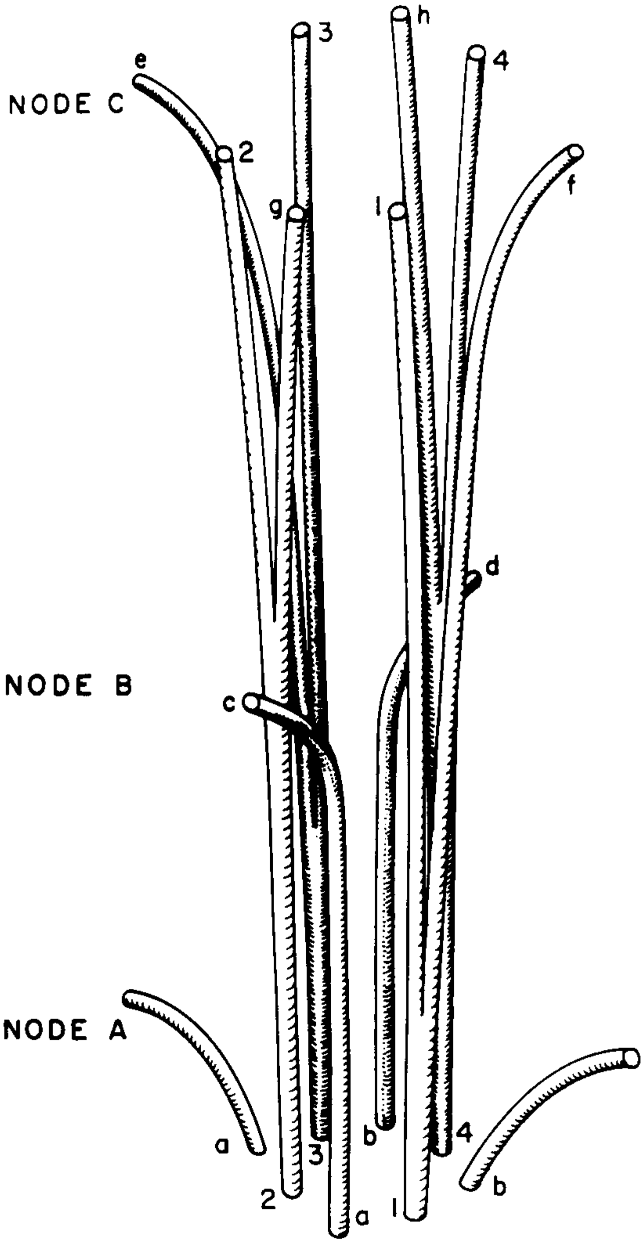

Fig. 1. Three-dimensional reconstruction of the primary vasculature of *Salicornia europaea* based on serial sections. Three nodes (A–C) are shown with opposite vascular traces alternating at 90° (a–b, c–d, e–f). Above Node A, six primary vascular traces ascend the main shoot axis. Two of these traces (c and d) diverge into Node B; four (1–4) continue up the internode. Approximately one-third to half way up the length of the internode, two traces each split to produce two more traces (g and h) that continue above Node C.

visible in transverse sections just above the node. The anatomy of each internode just above the subtending node consists of six traces. Two of these (Traces c and d) will diverge into the next higher node (Node B); two traces of the remaining four bisect further up the internode (1 bisects into 1 and 1f, 3 bisects into 3 and 3e). This results in eight primary vascular traces seen in transverse sections 1/3 to 1/2 up the length of internodes (Figs. 1 and 2).

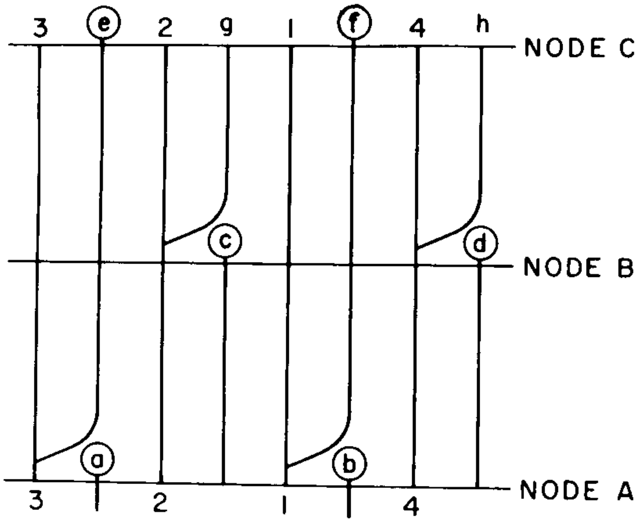

Fig. 2. Semi-diagrammatic version of Fig. 1 showing primary vascular traces of Nodes A–C and the two intervening internodes. Divergence angles between acropetally dividing vascular traces are exaggerated for increased clarity.

Two opposite traces (2 and 4) bisect above Node B to produce traces (g and h) that will diverge into the node above Node C. Thus, traces that diverge into nodes originate from other traces bisecting two internodes basipetally. These anatomical details are similar to those described by De Fraine (1912) and Fahn and Arzee (1959), although these investigators did not investigate branch traces.

The mean diameters of conducting tracheary elements found in traces ascending through main shoots and diverging into branches are shown in Fig. 3. Longitudinal sections through additional specimens revealed that these tracheary elements are vessel members and not tracheids or vascular fibers. Accordingly, we will refer to these elements as vessel members throughout the remainder of this paper. These data represent the sums of measurements taken through six specimens serially sectioned through two successive nodes and the intervening internode. Because the length of the specimens examined differed (1.1 ± 0.2 cm), the position of each measurement along the specimen has been normalized (i.e. a value of 1/2 on the abscissa denotes 1/2 the length of the internode). These traces have been labelled in the same fashion as those shown in Figs. 1–2.

The mean diameters of vessel members increase (1 and 3, e and f), decrease (2 and 4), or remain relatively unchanged (c and d) acropetally from Node A to Node B. Reduction in the diameters of vessel members within traces diverging into branches occurs just below the subtending node. For example, by referring to Figs. 1 and 3, vessel diameters in Traces 2 and 4 decrease in a region approximately 3/4 above Node A but bisect into g and h *above* node B (these g and h traces diverge into the node above Node C shown in Fig. 1). The vascular traces diverging into nodes show no significant re-

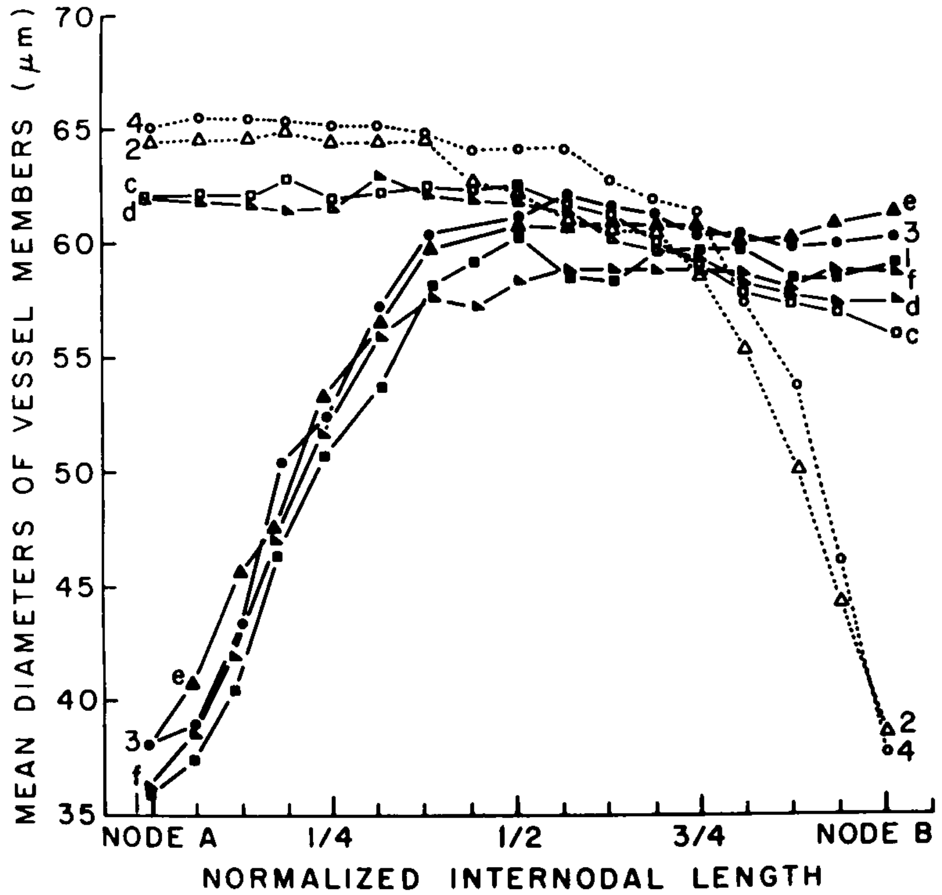

Fig. 3. Mean vessel member diameters (μm) of primary vascular traces through the internode between Nodes A and B (see Figs. 1 and 2). The length of the internode between Nodes A and B is represented as normalized fractions of internodal length (see text for details); vessel member diameters were compared in comparable regions determined by their fraction of total internode length. Vascular traces are keyed to Figs. 1 and 2 to provide geometric landmarks in anatomy.

duction in the diameter of their vessel members in the immediately subtending internode (Traces c and d in Fig. 3). Therefore, a node is associated with a region basipetal to it in which the diameters of vessel members decline; however, this decrease occurs in a region found two internodes below the node where the traces diverge.

We report mean vessel diameters in Fig. 3 for graphic convenience; Figs. 1–3 are not presented as an exact quantitative representation of the hydraulic architecture of *Salicornia*. Rather, these graphs provide a 'blueprint' useful in determining how plants should be dissected to determine flow rates of water through stem segments. Flow rate measurements (given below) provide the empirical evidence needed for determining the consequences and locations of vascular constrictions.

Water potential and resistance pressure measurements

In greenhouse grown plants, we observed that a significantly higher pressure had to be exerted to cause water to flow across nodes both on main stems and on primary branches (Table 1). However, main stem and primary branches did not differ in the pressures required to drive water from vessels within internodes (Table 1). That is, although the applied pressure increased precipitously across stem nodes, it did not decline significantly from the main stem towards the periphery of the plant. If water potential is similar throughout the plant, then nodal tissues must be in equilibrium with internodal water potential. Therefore, the higher pressures within the Scholander bomb needed to push water across a node were interpreted to reflect an anatomical resistance to water flow rather than a localized reduction in tissue water potential.

Internodal water potential was 3–15 times lower in stressed field grown plants (measured at midday) than in greenhouse grown plants (Table 1). Soil water potential, estimated in the field as the pre-dawn plant water potential was -2.65 ± 0.39 MPa ($n=20$), only slightly higher than the water potential of the stressed plants (Table 1). Unlike the greenhouse grown plants, however, the water potential at stem (branch) nodes in plants growing in the field was not significantly greater than the water potential within internodes (Table 1).

Flow rates

Flow rate of KCl within internodes was very rapid, ranging from 0.13 to 1.70 μl s^{-1} (Table 2), while flow rate across a node was almost undetectable (Table 2). Flow rate through a given stem segment was significantly corre-

Table 1
Pressure (MPa) required to push water out of vessel members of field and greenhouse grown *Salicornia* plants

Where grown[1]	*n*	On main stem[2]			On primary branch		
		Within internode		Across node	Within internode		Across node
Field	6	-2.9 ± 0.39	NS	-3.4 ± 0.32	-2.8 ± 0.29	NS	-2.6 ± 0.27
Greenhouse	19	-0.4 ± 0.22	*	-1.3 ± 0.25	-0.2 ± 0.15	*	-2.6 ± 0.26

[1] Greenhouse and field grown plants differed overall in water potential ($P < 0.01$, ANOVA).
[2] For both field and greenhouse grown plants, main stem and primary branch applied pressures were not significantly different within internodes, or across nodes.
For each growing location, pairs of significantly different values ($P < 0.05$, *t*-test with Bonferroni correction) are separated by an asterisk.

Table 2
Flow rates (μl s^{-1}) and fresh mass (g) of plant above the (inter)node where flow rate was measured. Only greenhouse grown plants were used for flow-rate experiments

Flow rate ($\bar{X} \pm$SD)	Mass above (inter)node	Where measured
0.23 ±0.088	0.485	within internode
0.13 ±0.068	0.560	within internode
1.70 ±0.280	1.005	within internode
0.25 ±0.121	0.575	within internode
0.31 ±0.111	0.515	within internode
0.0002±0.00008	0.250	across node
0[a]	0.455	across node
0[a]	0.663	across node

[a] After 90 min.

lated with the fresh mass supplied by the stem segment (r=0.84, $F_{1,6}$=14.51, P=0.009).

Discussion

We have documented the existence of regions within shoots associated with significant decreases in vessel member diameters in *Salicornia* xylem, and have shown that across these regions, fluid flow rates decrease by three orders of magnitude. This disproportionate change in magnitude of fluid flow rate relative to the decrease predicted from the decrease in vessel diameter (following the Hagen–Poiseuille equation; Zimmermann, 1983) suggests that much of the observed change in hydraulic conductance is due to factors other than vascular constrictions. The location of a disproportionate number of vessel end-walls in nodal regions could account for our results. Further studies of *Salicornia* anatomy are needed to address this hypothesis.

In greenhouse grown plants, the decrease in flow rate across these regions is accompanied by a significant increase in the applied pressure needed to cause water to flow through a node. However, a similar pressure gradient is not needed to cause water to flow across nodes in plants growing in the field. In plants grown under ideal conditions in the greenhouse, the observed increase in resistance across nodes parallels changes in patterns of water potential seen in palms and dicotyledonous trees. Tomlinson (1983) suggests that decreases in diameter of conducting tracheary elements diverging into branches is adaptive and would have appeared early in land plant evolution. If Tomlinson is correct, we would expect such decreases to be archaic, and to be present in most herbaceous plants. Our findings of regions of decrease in vessel member diameter in *Salicornia* (Fig. 3) and an increase in the applied pressure required to push water through these locations support Tomlinson's hypothesis.

The absence of an increase in water potential across nodes in field grown plants across nodes is puzzling, in light of the results obtained from greenhouse grown plants and the comparative data from other plant species. We suggest several reasons why the observed patterns of *Salicornia* water flow resistances in the field differ from predicted patterns.

The halophytic condition in the Chenopodiaceae is thought to be derived from a non-halophytic ancestor (Scott, 1977). Reductions in vessel member diameter may in fact reflect an adaptation to conditions of water stress (sensu Tomlinson, 1983) in the xeric habitat of many primitive chenopods. In more derived halophytic chenopods, such as *Salicornia*, that inhabit saline soils, the situation is very different, viz. very low negative pressures in xylem are needed to overcome the osmotic pressure of seawater (e.g. Waisel, 1972; Tomlinson, 1986), and water-use efficiency is low in these plants (e.g. Antlfinger and Dunn, 1983). In the hypersaline soils where *Salicornia* grows, the water potential may be so low in large vessels that relatively small decreases in water potential across vascular constrictions may be undetectable. The values for xylem water potential that we obtained for *Salicornia* in the field are almost identical with other published data for other *Salicornia* spp. (Kuramoto and Brest, 1979; Stumpf et al., 1986; Shumway, 1991). Studies of other halophytes have obtained similarly low xylem pressure potentials, ranging from -5.6 to -2 MPa (Scholander, 1968; Hadač and Hadačová, 1974; Antlfinger, 1981; Drake and Gallagher, 1984; Alpert, 1990; Shumway, 1991). We therefore have no reason to suspect that our field results are somehow aberrant, although in none of the aforementioned studies did the authors measure water potential at different locations throughout the plant.

Zimmermann (1983) estimated that a decrease of 0.01 MPa m^{-1} in water potential is needed on average to maintain fluid flow in trees, and Begg and Turner (1970) found a decrease of 0.08 MPa m^{-1} with increasing height in tobacco. *Salicornia* is a short plant (under 50 cm), and significant decreases in water potential may not be needed to maintain continuous water flow to peripheral stems. If so, relatively wide vessels throughout the plant to maintain relatively high flow rates would not be selectively disadvantageous.

The vascular anatomy of *Salicornia* differs from that of trees and palms in that vessel member diameter in *Salicornia* decreases only locally; vessel diameter is equally wide on either side of the constriction. The existence of decreases in vessel member diameter in *Salicornia* at xylem bifurcations may be solely a consequence of axillary bud development. During the early growth of a bud when the shoot apex establishes itself, xylem initials may produce significantly smaller and narrower vessel members. Aloni and Zimmermann (1983) demonstrated that the rate of vessel differentiation in beans (*Phaseolis vulgaris* L.) is controlled by auxin concentration, and showed that high auxin concentration (such as occurs at growing tips) results in the rapid production of numerous, narrow vessels while decreased auxin concentration (basipetal to growing tips) results in slower production of fewer, wider vessels.

The diameters of early- and late-maturing vessel members differ, and as a result the conductance of water through vascular traces would be expected to differ depending on the developmental age of nodes and internodes. Our data, based on mature individuals (those that have ceased elongation and the production of new branches) reflect the hydraulic architecture of *Salicornia* throughout the majority of its lifespan. The vessel diameters we measured included those of the protoxylem and metaxylem (early and late vessel members). Clearly, 'bud activation' would involve early (smaller diameter) and late (larger diameter) vessel members with a concomitant shift from relatively high to lower resistances to water flow in vascular traces. Consequently, our data are a conservative assessment of the hydraulic consequences of vascular constrictions experienced during early ontogeny. Interestingly, the shift from high to low resistance attending the ontogeny of a branch would be concomitant with a shift from a low to a high transpirational area as the branch increased in size. This discussion illustrates that developmental processes can give rise to decreases in vessel member diameter that are independent of an adaptationist scenario related to vascular constrictions, although the adaptationist model of hydraulic architecture is not refuted by our data. However, we would suggest that ontogenetic reductions in vessel diameter may represent an exaptation (sensu Gould and Vrba, 1982) in early vascular plants that has, because of its adaptive value in more xeric conditions, been subject to strong selective pressures over evolutionary time.

The location of the hydraulic constrictions in *Salicornia* differs from that found in trees and palms. The vascular constrictions in *Salicornia* stems are two nodes below the morphological emergence of a branch. Because vessel members have lateral wall perforations through which water can flow, the absence of a dramatic decrease in resistance to water flow at branch nodes suggests that lateral water flow above the constriction is of sufficient volume to bypass the effect of (a basipetally located) 'constriction' of longitudinal flow. This observation, while not refuting the hydraulic model (Tomlinson, 1983; Zimmermann, 1983), highlights the complexity seen in the anatomy of *Salicornia*, and the need for further study of the relationships between water relations and the physiology, anatomy, development, and field ecology of many plants of diverse morphologies.

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