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XYLEM ANATOMY, WATER FLOW, AND HYDRAULIC CONDUCTANCE IN THE FERN CYRTOMIUM FALCATUM[1]

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ABSTRACT

Xylem anatomy and water relations were studied in holly fern (*Cyrtomium falcatum*, Aspidiaceae) to determine the details of the pathway for water flow through an entire plant and the influence of tracheid number and lumen diameter on water flow. Each leaf has two adaxial traces and an abaxial trace, which are supplied by diarch adventitious roots attached to the dictyostele of the rhizome near the leaf base. Anatomical observations and dye experiments showed that each adaxial bundle vascularizes the approximately seven pinnae on its side of a leaf. An abaxial bundle is intermittently connected to an adaxial bundle as well as other abaxial bundles, forming a minor vascular pathway between the bundles of the leaf axis. Changes in both number and diameter of tracheids result in an acropetal decrease in hydraulic conductance per unit length along the rachis, although tracheid number locally increases when the trace for a pinna is produced in an adaxial bundle. Water flow was determined from the transpiration distal to the point in question or by forcing a solution through an axis with applied pressure. The water potential gradient along the plant axis was quite constant, indicating that hydraulic conductance per unit length varied with leaf area to be supplied. About 40% of the overall water potential drop occurred from the rachis into the pinnae, which reflected factors controlling water potential gradients in the lamina and not a very low conductance in the petiolule xylem. Hydraulic conductances calculated using the Hagen-Poiseuille equation and tracheid diameters were generally double those of measured conductances. Since the values tended to vary by a constant factor, tracheid number and diameter may largely control water flow in the xylem.

WATER MOVEMENT in vascular plants occurs mainly through the elongate conduits of the xylem—vessels or tracheids—because at maturity they offer the pathway of maximum hydraulic conductance. Water flow is more rapid in vessels than in tracheids and in wide rather than in narrow conduits (Huber and Schmidt, 1936, 1937; Huber, 1956; Zimmermann, 1971, 1983; Milburn, 1979). A vessel should be a more efficient conduit than a series of tracheids, because water in a vessel does not have to flow through the cell walls between vertical xylary elements (Bailey, 1953; Carlquist, 1975). Wider conduits permit greater flow because, according to the Hagen-Poiseuille law, conductance per tube is proportional to capillary diameter raised to the fourth power (Zimmermann, 1971, 1983; Nobel, 1983). Xylem influences on water flow in whole plants can best be understood by studying the entire liquid-vapor conductance network from the soil-root interface through the plant to the leaf surface. Tree physiologists have recognized the need for such holistic analyses to explain water transport (Hinckley, Lassoie and Running, 1978), and various workers have examined plant and leaf conductances in relation to water flux (e.g., Johnson and Caldwell, 1976; Nobel, 1978; Nobel, Longstreth and Hartsock, 1978; Black, 1979b; Blizzard and Boyer, 1980; Woodhouse and Nobel, 1982).

To understand the relationship between water flow and xylem structure, the volume of water flowing per unit time is often determined. Early studies used dyes and thermo-electric (heat-pulse) techniques to measure the velocity of sap ascent in woody stems (Huber and Schmidt, 1936, 1937; Zimmermann, 1971, 1983), but uncertainties are introduced since water moves at different rates through the center as opposed to the periphery of a conduit and through conduits of different sizes. Consequently, methods that label only the water front cannot readily quantify the volume flowering per unit time, q, which is needed for calculations of conductance and comparisons with xylem anatomy. Through a portion of the plant axis, q ($m^3\ s^{-1}$) is determined by the hydrostatic pressure drop ΔP (MPa) and the hydraulic conductance k_h ($m^3\ MPa^{-1}\ s^{-1}$):

$$q = k_h \Delta P = K_h \frac{\Delta P}{\Delta x}, \qquad \text{Eqn. 1}$$

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where $\Delta P/\Delta x$ is the pressure gradient and K_h is the hydraulic conductance per unit length ($m^4\ MPa^{-1}\ s^{-1}$). The parameters k_h and K_h for different plant parts may then be calculated from measured flows and local hydrostatic pressures along each part. The value of K_h may also be estimated from anatomical measurements using the Hagen-Poiseuille law:

$$q = \frac{\pi \sum^{n} d_i^4}{128\eta} \frac{\Delta P}{\Delta x}, \qquad \text{Eqn. 2}$$

where d is the diameter (m) of the i^{th} tracheid or vessel in a cross-section and η is the viscosity of water (MPa s) (Woodhouse and Nobel, 1982; Nobel, 1983). Equation 2 is based on the characteristics of laminar flow in ideal, long, horizontal, constant-diameter tubes and often underestimates the gradient required due to deviations of real systems from the assumptions, but it does indicate the important influences of tracheid number and especially diameter (Zimmermann, 1971, 1983; Giordano et al., 1978; Petty, 1978). Hence, it is crucial to obtain cell diameters and other xylem features to relate structure to function.

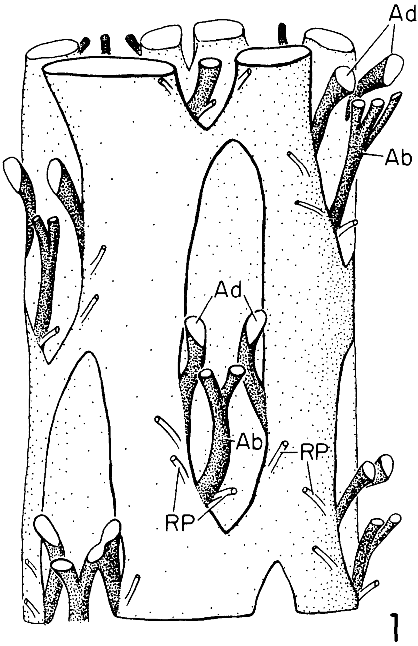
Ferns are good subjects to investigate the relationship between conductances and xylem structure. Most ferns have no secondary xylem and only tracheids, whereas the course of water movement in seed plants is complicated by secondary growth (gymnosperms and dicotyledons) or is more complex to model due to the presence of both vessels and tracheids (some monocotyledons and dicotyledons). Certain ferns have very high water potential gradients (Nobel, 1978), and preliminary studies have shown that tracheid diameter and number correlate well with xylem hydraulic conductance (Woodhouse and Nobel, 1982). However, no fern study has calculated conductances at various locations along the vascular network, and so local effects of xylem structure on water flow have not been determined.

This study seeks to understand the effects of xylem structure on sap flow in holly fern, *Cyrtomium falcatum* L. f. (Aspidiaceae). This is an easily cultivated, rapidly growing species with an uncomplicated vascular system and a relatively high stomatal conductance. As its name implies, holly fern has fronds with holly-shaped pinnae that are suitable for use with standard ecophysiological equipment.

MATERIALS AND METHODS—*Cyrtomium falcatum* is a terrestrial fern native to temperate eastern Asia. The short, erect, epigeal rhizome is covered with numerous persistent, wiry roots with new roots arising between upper leaf bases. Leaves are once pinnately compound, consisting of a stipe (petiole) and rachis with a pair of lateral lines containing stomata (Ogura, 1972) and usually with 11–17 pinnae that tend to be arranged in a subopposite fashion beginning 12 cm from the base, and becoming alternate near the termination of the rachis, which bears a single pinna. Lateral pinnae are somewhat coriaceous and narrowly to broadly ovate, 4–8 cm long by 2–4 cm wide, with entire to dentate margins, oblique bases, and long acuminate apices. The terminal pinna is often wider and may be deeply cleft or lobed. Petiolules are 0.2 to 0.5 cm long.

Plants of the holly fern were obtained from the Hannah Carter Japanese Garden of the University of California, Los Angeles, California. They were subdivided to make specimens consisting of a 3-cm-long rhizome bearing several mature leaves (fronds) approximately 30 cm long. These were planted in a soil mixture of 1 part each of sand, sandy loam, and peat moss, 3 parts vermiculite, and 0.003 parts hoof-and-horn meal to provide micronutrients. Specimens were watered daily with $\frac{1}{10}$ Hoagland solution no. 1 to avoid water stress (Prange and Ormrod, 1983). The plants were maintained in a greenhouse under natural light that averaged over 11 mol m^{-2} day^{-1} photosynthetically active radiation (PAR) with a daily maximum of about 1,000 μmol m^{-2} s^{-1}, both measured on a horizontal surface. Pinnae thus received PAR leading to at least 90% saturation of photosynthesis and stomatal opening (Gibson et al., in press) for 7 hr daily. Each leaf produced under these conditions had a total area of 243 ± 23 cm^2 (S.E. for $n = 9$). During physiological experiments on fully expanded hypostomatic leaves without mature sori, plants were maintained at 600–800 μmol m^{-2} s^{-1} PAR, 25–28 C, and an air water vapor pressure of 1.7–2.3 kPa. Under these conditions, leaf conductance to water vapor diffusion averaged 1.6 mm s^{-1}, resulting in whole leaf transpiration rates of 309 ± 14 μg s^{-1} (S.E. for $n = 21$).

Vasculature of a sporophyte was studied to demonstrate the pathway of water in the xylem from roots to pinnae. Rhizome tissues were preserved in formalin-acetic acid-ethanol (FAA) fixative (Johansen, 1940), dehydrated through a tertiary butanol series, and embedded in Paraplast. Serial transections cut at 30-μm intervals were stained with safranin or safranin and fast green. The mature stele was then reconstructed with emphasis on the attachment of leaf-trace bundles and root vasculature. For describing vasculature of the leaf axis,



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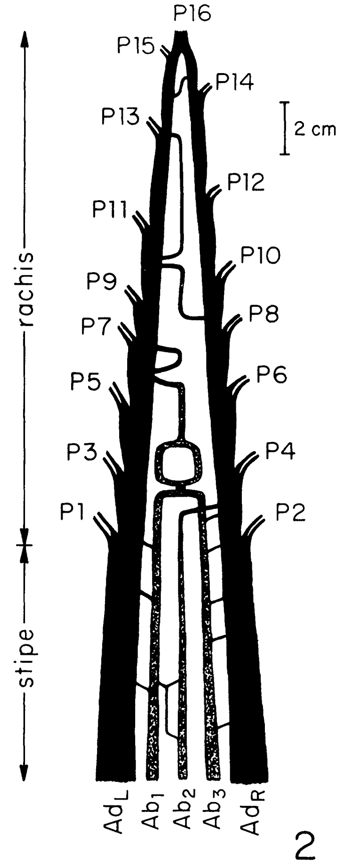

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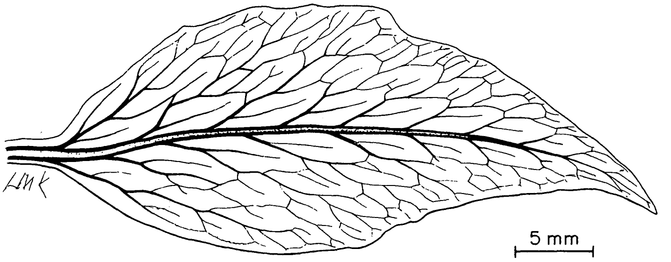

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Fig. 1–3. Primary vasculature of *Cyrtomium falcatum*. **1.** Segment of the dictyostele of a rhizome, showing the origin of adaxial (Ad) and abaxial (Ab) leaf traces as well as the splits and fusions of bundles within the first several millimeters after departing the stele. Attachment of root protosteles (RP) is also shown. This stele is drawn to scale in the horizontal but is greatly expanded in the vertical plane to show the basic design. **2.** Diagrammatic adaxial view of leaf trace bundles beginning 3.0 cm from the dictyostele. This leaf has two major adaxial bundles, Ad_L (left) and Ad_R (right), and a system of smaller abaxial bundles (Ab_1, Ab_2, Ab_3), which would be connected to the node in the upper right of Fig. 1. Adaxial bundles are spread laterally to reveal the underlying abaxial bundles. The stipe-rachis axis is shown to scale longitudinally, indicating where a trace diverges for each pinna (P1–P16). Width of all bundles is drawn to show relative diameters and that adaxial bundles have regular oscillations in number of tracheids. **3.** Venation of a typical lateral pinna (petiolule and lamina).

three leaves having 12, 16, and 16 pinnae were chosen, and thin freehand serial transections of fresh tissue were made along the entire axis (about 30 cm long), noting where bundles fused or were connected by short bridges, overall changes in bundle size and shape, the origin of the trace to each pinna, and the nature of each vascular fusion. Venation was studied for sterile pinnae cleared in 1.2 M NaOH and stained with safranin, using images projected from a photographic enlarger.

Patterns of water flow were studied by introducing dyes into vascular bundles within the stipes of transpiring excised leaves. Acid fuchsin, eosin, and methylene blue were all used with similar results (Roach, 1939). Stipes were cut and recut under water, and the basal 2 cm was split longitudinally into a portion containing the bundle or bundles to be placed into 0.1% dye solution and a portion to be placed into water. After 10 min, transverse cuts were made along the stipe, rachis, and petiolules and examined under a stereomicroscope to determine which bundles were stained. Steady-state water flow through intact plants was calculated from transpiration of whole pinnae placed in a Li-Cor LI-1600-02A cylindrical chamber used with a Li-Cor LI-1600 porometer. Flow through any portion of the plant axis was assessed by summing the transpiration of all pinnae distal to that portion, ignoring transpiration from the leaf axis (stipe and rachis).

Xylem water potentials at various locations were estimated after covering pinnae or entire leaves and assuming that the covered portions attain equilibrium with the xylem at the point of petiolule or stipe insertion, respectively (Begg and Turner, 1970; Black, 1979a). Water potentials were measured with a Scholander-type pressure bomb, loss of water from pinnae or leaves after excision being limited by covering them with aluminum foil and by humidifying the pressure chamber with a wet paper towel. Soil water potential was measured with thermocouple psychrometers and estimated by measuring leaf water potential of whole plants whose leaves were covered by aluminum foil before placing the entire plant in a plastic bag. Water potentials of severed root tips were also measured in the pressure chamber.

Hydraulic conductances of 1–4 cm lengths of roots and stipes and of petiolules were measured by forcing a 20 mM KCl solution through excised portions with an imposed pressure gradient of 21 kPa (Zimmermann, 1978; Giordano et al., 1978). Flow was measured by continuously collecting the exudate with a syringe, which resulted in very little loss by evaporation (Calkin and Pearcy, in press).

For comparing water potential gradients with xylem anatomy, tracheid number and lumen diameter were determined from paraffin-embedded portions of roots and leaves serially sectioned at 15-μm intervals and stained with safranin, or from thin, unstained, freehand transections of fresh plant parts. Fresh sections were dried on a microslide until the majority of tracheids had drawn in air and then mounted in corn oil. This permitted easy identification of tracheids using a light microscope, because they were clear and their secondary walls with marked layering and birefringence under polarized light readily distinguished them from xylem parenchyma and primary phloem. Diameters for the conducting area of each tracheid were determined with an ocular micrometer for the largest circle that could fit within the tracheid lumen. Because lumens of fern tracheids are generally angular or somewhat elongate, actual area averaged 56% larger than this circular area, as determined from photographic enlargements of xylem transections.

RESULTS—*Description of vascular system*—The mature vascular system of the short erect rhizome is a radially symmetric dictyostele having leaf traces and leaf gaps conforming with a 2/5 phyllotaxy (Fig. 1). Three traces vascularize each leaf primordium. The lowest one diverges into the abaxial region of the leaf axis. The other two traces diverge from the dictyostele into the adaxial region of the leaf axis at a slightly different level about halfway through the leaf gap, and they function as the two principal leaf bundles. The two adaxial traces do not fuse laterally and hence remain discrete until they converge in the distal 1–2 cm of a leaf, where they fuse in the vicinity of the penultimate pinna (Fig. 2). Each pinna receives a single trace from the nearest adaxial bundle, so that most of the water for the pinnae on the right half comes from the right adaxial bundle, and the left adaxial bundle vascularizes the left side.

The course of the abaxial bundle in any leaf is variable (Fig. 2). The original bundle, which splits within 1.5 mm into two bundles, experiences further splits resulting in up to 5 bundles in the stipes of large leaves, as well as having many subsequent fusions. At fairly regular intervals, the left and right lateral abaxial bundles alternately fuse for up to 100 μm with their respective adaxial bundle as the smaller abaxial bundle differentiates toward the larger adaxial one. In the stipe the lateral abaxial bundle can also form a narrow vascular bridge to its adaxial counterpart. Usually only two abaxial bundles occur in the upper stipe and midway through the rachis abaxial vasculature is reduced to a single strand. This single bundle may temporarily fuse with and then diverge from an adaxial bundle until the abaxial system permanently fuses with one adaxial bundle in the vicinity of the subterminal pinnae.

After departing from an adaxial bundle, a trace immediately dichotomizes to produce two bundles which become the midvein of a pinna (Fig. 3). The smaller secondary bundles diverging from the two main bundles divide unequally several times in an alternating fashion before reaching the pinnal margin. In the differentiation of minor veins, the secondary bundles are interconnected as a reticulum by the production of bridges to form the areoles. Each areole has a blindly ending vein, which terminates where a sorus may develop.

Adventitious roots emerge from the rhizome between leaf primordia, except very near the apical dome. Each root protostele is attached directly to vascular tissue in the dictyostele of the rhizome. A root develops upward as it grows outward until the root cap protrudes from the rhizome, when positive geotropism is expressed. In any 30-μm transection of a rhizome there are about 15 distinct roots in the cortex and 5 or more just diverging from the stele. In the meristelic region between adjacent leaf gaps there are at least three roots. One root typically diverges within 100 μm and directly proximal to the abaxial leaf trace, suggesting an intimate developmental and functional relationship between this root and a leaf.

Dye experiments—Introduction of dye solutions into one of the adaxial bundles in the lower stipe of a transpiring leaf resulted in staining of xylem tissue in the distal portion of that bundle, including the traces to all pinnae on that side of the leaf axis. Abaxial bundles were stained distal to a divergence from such an adaxial bundle. No staining was detected in the opposite adaxial bundle, except when the occasional merging of a stained abaxial bundle with this second adaxial bundle led to localized staining there. Severing the unstained adaxial bundle distal to the level at which dye was introduced resulted in staining this bundle distal to the cut, presumably reflecting movement in associated abaxial bundles. In response to severing an adaxial bundle, xylem tensions were increased by 0.42 ± 0.05 MPa (S.E. for $n = 8$) on the cut side and by 0.25 ± 0.05 MPa on the intact side (determined from the water potentials of covered pinnae on the respective sides). Thus, a water potential gradient of about 0.17 MPa was established between the adaxial bundles, which led to the observed lateral transport of dye solution. Dye introduced into abaxial bundles eventually stained both adaxial bundles.

Xylem anatomy—The number of tracheids in each bundle changes along the leaf axis. At the base of a stipe the xylem has a hippocampus form (Ogura, 1972) with adaxial and abaxial hooked ends facing inward. A transection there has over 1,000 tracheids, about one-third of which occur in the 2 or 3 abaxial bundles and one-third in each of the two adaxial bundles. Further up the leaf axis the hook is lost from the abaxial bundles. Wherever an abaxial bundle temporarily fuses with an adaxial bundle, the two xylem regions also fuse and so the number of tracheids in the adaxial bundle is then approximately the sum of the two. In middle and upper stipe, tracheid number decreases to 500–700 per transection, and a smaller fraction of tracheids occurs in the abaxial system. In the lower rachis immediately before the divergence of a trace to a pinna, tracheid number increases to 800; about 40% of the tracheids from the appropriate adaxial bundle then diverge into the petiolule, so that just after the trace divergence about 650 tracheids occur in a transection (Table 1). In the next interpinnal interval the number of tracheids returns to about 750. The adaxial bundle on the side opposite a trace begins the series at an intermediate point, from which tracheid number gradually increases to provide the trace for the next pinna, where its maximum number is reached. The number of tracheids midway through each interval gradually decreases along the rachis until only 250–350 tracheids occur in the upper rachis (distal to the 12th pinna; see Table 1) and less than 150 in the portion of the axis entering the terminal pinna. In any transection less than 25% of all tracheids occur in the abaxial bundles, increases of about 15–20 narrow tracheids occurring when bridges are formed with adaxial bundles.

At all levels in the axis, over 60% of the tracheids in a transection are less than 10 μm in diameter. This percentage increases prior to the divergence of a trace to a pinna and may become 90% in the uppermost part of the rachis (Table 1). Most of the remainder are also narrow; e.g., in a transection taken anywhere in the stipe or midway between petiolules along the lower rachis, 19–30% of the tracheids are 10–20 μm in diameter. The most interesting pattern occurs in the larger size classes. The percentage of tracheids 20–30 μm in diameter is fairly constant along the leaf axis and decreases only in the uppermost rachis, but the largest tracheids (>30 μm) are absent from the base of the stipe, increase to a maximum in the middle and upper stipe (max. 50 μm), and then decrease linearly with distance until they are no longer present in the upper rachis. Tracheids greater than 30 μm in diameter do not occur in abaxial bundles. The trace that vascularizes a pinna usually has 90–170 small tracheids, the diameter of the widest tracheid being less than 20 μm. Neither diameter nor number of tracheids varies much within the petiolule. Following the departure of a pinnal trace, an adaxial bundle has half the number of tracheids over 10 μm in diameter, and this number may drop somewhat through the next interval since

TABLE 1. *Tracheid number and calculated hydraulic conductances per unit length for transections through a segment of an uppermost stipe and a lower, middle, and upper rachis. For each set of transections, a trace diverged first to the left into a pinna (pinnae 1, 5, and 11, respectively) and the next one to the right. For each bundle number of tracheids in each size class is noted*

Interval and position in the interval[a]	Number of tracheids									Hydraulic conductances per unit length (m^4 MPa^{-1} s^{-1} × 10^{-12})			
	Left adaxial bundle			Right adaxial bundle			Abaxial bundles[b]			Left adaxial bundle	Right adaxial bundle	Abaxial bundles	Total
	<10 μm	10–20 μm	>20 μm	<10 μm	10–20 μm	>20 μm	<10 μm	10–20 μm	>20 μm				
LOWER RACHIS													
Stipe distal	298	73	26	206	57	24	156	34	1	441	456	46.7	1,164
1–2 proximal	151	40	24	270	57	22	168	33	0	396	496	58.9	951
MIDDLE RACHIS													
4–5 distal	267	99	19	201	51	19	106	19	1	353	356	31.2	741
5–6 proximal	111	51	25	223	58	24	89	16	0	496	346	25.5	867
5–6 median	143	48	21	216	52	15	93	15	0	364	361	24.6	750
5–6 distal	202	47	22	306	96	28	84	13	3	378	382	44.6	805
6–7 proximal	190	42	21	142	43	17	58	14	0	321	258	22.1	600
UPPER RACHIS													
10–11 distal	277	56	4	133	34	6	52	9	0	125	95	12.2	232
11–12 proximal	112	27	6	145	31	7	54	4	0	122	80	8.8	211
11–12 median	119	23	7	175	31	5	73	7	0	80	114	10.5	204
11–12 median-distal	150	17	4	178	35	3	46	4	0	73	82	5.5	160
11–12 distal	139	21	5	241	46	6	60	4	0	122	85	5.9	213
12–13 proximal	134	18	4	89	21	4	44	3	0	77	76	4.7	158

[a] Intervals are defined as the axis section between two successive pinnae, e.g., interval 1–2 is the region between pinna 1 (lowest) and pinna 2. Sections were made just below departure of a trace (distal in a particular leaf axis interval), just above departure of a trace (proximal) in a particular leaf axis interval, or midway between two petiolules (median).

[b] Sections of the upper rachis had only one abaxial bundle.

there is a gradual reduction of large tracheids along the leaf axis.

Roots with fully differentiated diarch xylem have only 35–55 tracheids, three or four generally having diameters greater than 30 μm. The thickest tracheid walls in the entire plant (9 μm) occur in root metaxylem elements. There is no apparent difference in the lateral-wall pitting of root and leaf tracheids, which is scalariform with pit apertures only about 2 μm in diameter.

Water relations and hydraulic conductance—The local average water potentials of transpiring plants illustrate the water potential gradients along the plant axis (Fig. 4). The gradient was quite constant from a water potential of −0.19 ± 0.01 MPa (S.E. for $n = 13$) at the root tips to −0.58 ± 0.04 MPa ($n = 10$) at the distal end of the rachis. This water potential drop of 0.39 MPa occurred over a distance of about 45 cm. The greatest water potential gradients occurred between the rachis and the site of evaporation in the laminae of the pinnae, a distance averaging 3.1 cm, where about 0.27 MPa, or 40% of the total water potential drop from the soil to the pinnae occurred.

The water potential drops and water flows through each part of the plant allowed estimation of the conductance at each level of the soil-plant-air continuum (Fig. 5). Root and stipe conductances were quite similar and averaged 33% higher than the soil conductance. The laminar network conductance includes the conductance along the rachis and from the rachis through the pinnae, the latter representing parallel pathways; its relatively small value (Fig. 5) results largely from the very small conductance from the rachis through each pinna of 0.11 ± 0.01 (S.E. for $n = 45$) × 10^{-9} m^3 MPa^{-1} s^{-1}.

Conductances per unit length were further analyzed along the stipe and rachis (Fig. 6). The value of K_h was fairly constant over the length of the stipe, but it decreased at each rachis node, where a portion of the total flow is diverted toward a pinna. The amount of flow diverted to a given pinna was largely determined by pinnal surface area, since there was no consistent trend of stomatal conductance among pinnae inserted at different points along the rachis. Dividing K_h of each rachis section by the pinnal area distal to that section yields a more constant value (Fig. 7). The somewhat

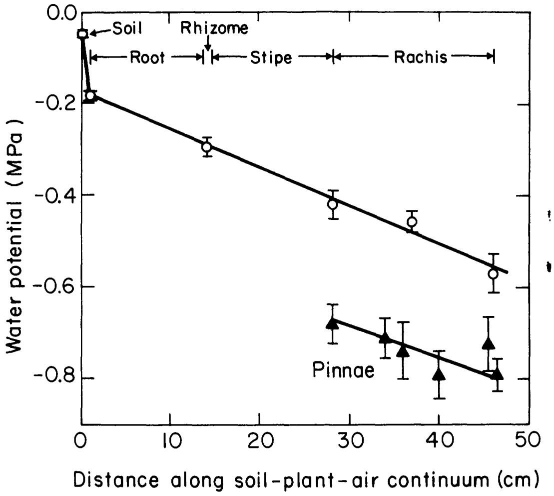

Fig. 4. Water potential gradient along the soil-plant-atmosphere continuum. Circles represent water potentials along the axis of the plant from soil and root through rhizome and stipe to the rachis. Triangles represent water potentials of pinnae, and are plotted at the point of insertion along the rachis. The root length on the abscissa is the distance from base to tip of the longest roots. The distance from root tip to bulk soil is shown as 1 cm, the approximate distance from root tips to the soil probes. Data are plotted as means ± S.E. for at least six measurements in each case.

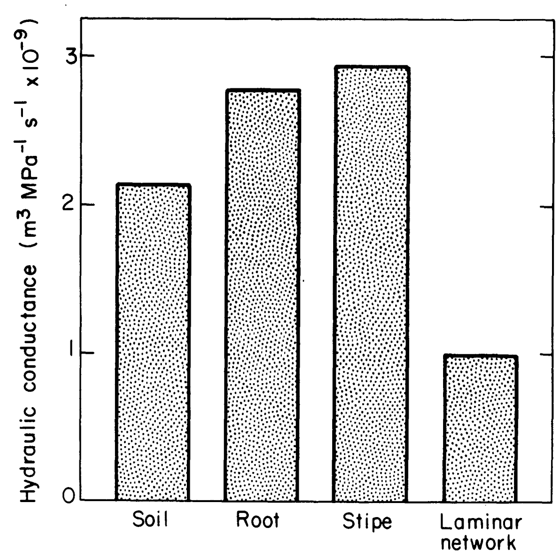

Fig. 5. Soil, root, stipe, and laminar network conductances to water flow calculated from water potential gradients and the rate of water flow per unit leaf area. Laminar network conductance is a combination of individually measured series conductances along the rachis and parallel conductances to individual pinnae.

lower conductance per leaf area supplied for the upper part of the rachis resulted in slightly but consistently higher water potential gradients there (paired observation t test; $P < 0.025$).

The hydraulic conductances per unit length of individual roots are about 19% as large as stipe values (Table 2). Petiolule conductances per unit length are only about 1.0% as large as stipe values, even though flow through a typical petiolule is 7.1% of the flow through a stipe. Conductances per unit length calculated from Equation 2 are twice as high as measured values (Fig. 6; Table 2) over the 15-fold range of magnitude observed in the root, stipe, and rachis. The much smaller calculated conductances of petiolules were 4.8 times the measured values (Table 2).

DISCUSSION—The vascular system of the rhizome of *Cyrtomium falcatum* is a dictyostele with each leaf vascularized by two major adaxial trace bundles having hippocampus-shaped xylem and one abaxial trace, a trace diverging singly and abruptly from an adaxial bundle into each pinna. This design is characteristic of many terrestrial Aspidiaceae (Ogura, 1972), although some taxa assigned to this family, e.g., *Bolbitis* and *Egenolfia* (Nayar and Kaur, 1965), have additional pairs of traces. In some ferns, individual roots are closely associated with a specific leaf (Lachmann, 1888), and in *C. falcatum* at least one of the roots departs directly beneath the abaxial leaf trace. Dye experiments verify that water moves to pinnae on each side of a leaf chiefly from the adaxial bundle on that side, and there is normally little apoplastic transfer of water between the two adaxial bundles. Such separation has been seen anatomically (Bell, 1934) and in patterns of movement in different tracers in herbaceous species (Roach, 1939; Lal, 1945) and in trees (Koz-

TABLE 2. *Hydraulic conductances of roots, stipes, petiolules and pinnae obtained from pressurized flow through segments and from Hagen-Poiseuille calculations. Root sections were taken near the rhizome and basal to any branch roots. Pressurized flow samples of petiolules included the junction to the rachis adaxial trace. Tracheid diameters for pinnae were taken from transections of the midvein, bisecting the area to be supplied. Data are presented as mean ± S.E. (number of measurements)*

	Hydraulic conductance per unit length (m^4 MPa^{-1} s^{-1} × 10^{-12})	
	Pressurized flow	Poiseuille calculation
Root	96 ± 16 (7)	192 ± 21 (7)
Stipe	500 ± 72 (12)	900 ± 120 (6)
Petiolule	4.8 ± 0.4 (13)	23.2 ± 2.3 (7)
Pinna		9.7 ± 1.3 (6)

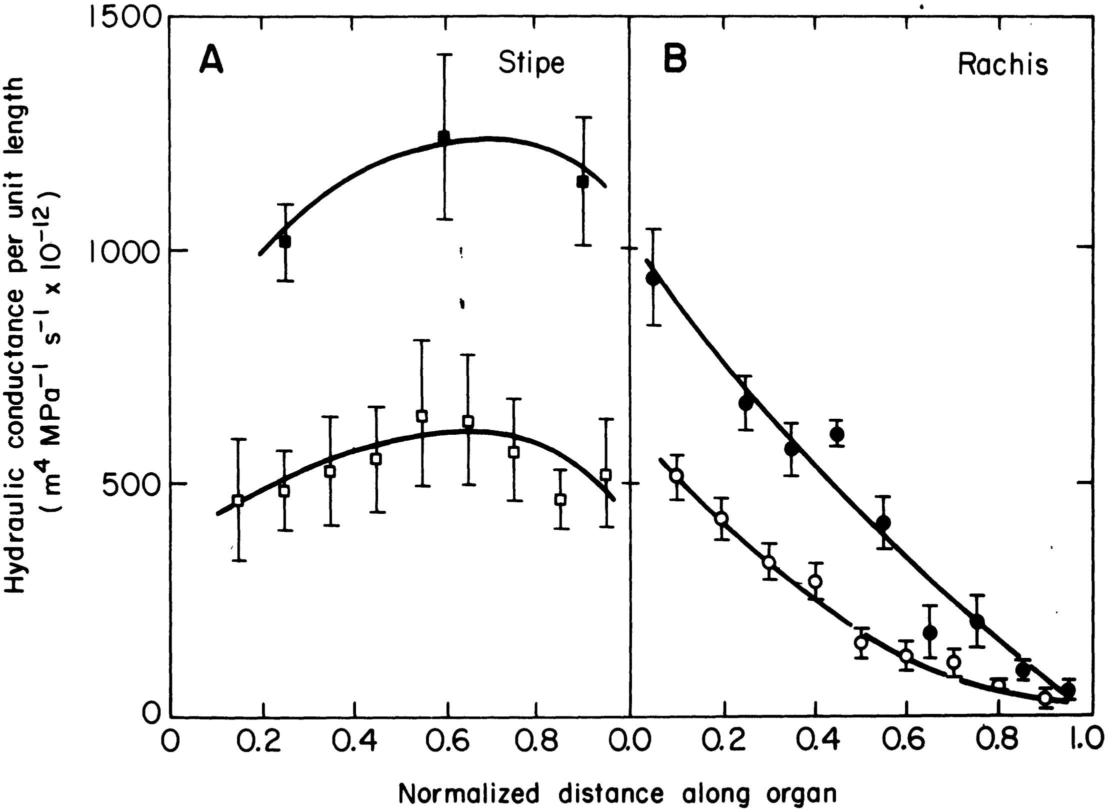

Fig. 6. Hydraulic conductance per unit length at different intervals along the stipe (A) and rachis (B). Closed symbols represent calculations from tracheid diameters using Eqn. 2. Open squares are conductances determined by forcing 20 mM KCl through excised stipe sections. Open circles depict K_h of rachis internodes calculated from water potential gradients and water flows measured on intact plants. Data are means ± S.E. for at least six measurements within a span of 10% of overall length.

lowski and Winget, 1963). The minor connections between adaxial and abaxial bundles permit some flow from one adaxial bundle to the other, however, and so flows, gradients, and conductances must be considered for the leaf axis as a whole, rather than for the two sides separately.

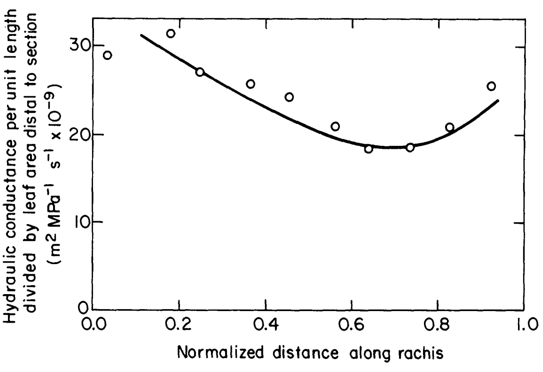

Fig. 7. Rachis hydraulic conductance per unit length, calculated from water potential gradients and water flows measured on intact plants, divided by total leaf area distal to that internode.

The water potential gradient along the stipe and rachis of *C. falcatum* of about 0.9 MPa m^{-1} contrasts with gradients ranging from 2.3–24.6 MPa m^{-1} for stipes of certain other ferns (Woodhouse and Nobel, 1982). Excepting the tree fern *Alsophila australis,* the conductance per unit length of the stipes of these ferns was only 2.5–10% of the values for *C. falcatum.* The conductance per unit length of *A. australis,* which has many large tracheids and a large leaf area, was 8.2 times that of *C. falcatum,* illustrating the wide range for ferns. Ferns in general have smaller conductances than do seed plants. On a leaf area basis, whole plant conductance from root tip to site of water evaporation in the lamina of *C. falcatum* was 40–75% of that for *Capsicum annuum* (Janes, 1970), 25% of that for *Helianthus annuus* (Black, 1979b), and 20–26% of that for *Vigna sinensis* (Hailey et al., 1973). This resulted in similar water potential drops for higher transpiration rates in the seed plants. The conductance of the root systems of these seed plants ranged from 1.9–2.8 times the whole plant conductance (Black, 1979b; Boyer, 1969; Jensen, Taylor and Wiebe, 1961), and it was 2.5 for *Lycopersicon esculentum* (Jensen et al., 1961). In *C. falcatum,* the root conductance was 4.8 times the whole plant conductance, indicating that although the whole plant conductance was lower, the root system conductance of *C. falcatum* was slightly higher than in the forenamed seed plants.

The fairly constant water potential gradient from root tip to end of the rachis suggests that hydraulic conductance per unit length is fairly constant along the root, rhizome, and stipe, and then varies in concert with the leaf area to be supplied along the rachis. Because main roots have many branches and therefore water absorption regions are diffuse, the root system forms a network analogous to that of the laminar network. This was not analyzed in detail here nor was the distance from root absorbing surfaces to the bulk soil accurately determined. Nevertheless, K_h of roots averaged 96×10^{-12} $m^4\ MPa^{-1}\ s^{-1}$, and there were at least 3–5 roots associated with each leaf; their total hydraulic conductance per unit length of 290×10^{-12} to $480 \times 10^{-12}\ m^4\ MPa^{-1}\ s^{-1}$ is similar to that of the stipe ($500 \times 10^{-12}\ m^4\ MPa^{-1}\ s^{-1}$). Since the conductances measured for sequential intervals of stipe yield a total conductance matching that measured for the whole stipe in intact plants including the rhizome-stipe junction, the latter is apparently not a physiologically significant constricted zone (Isebrands and Larson, 1977; Larson and Isebrands, 1978) in *C. falcatum.* Similarly, the large water potential drops between the rachis and pinnae are not due to a localized constricted zone, but to lower xylem conductances throughout the short petiolules and the laminae.

Throughout the study, a median transection of a rachis interval was used to compare xylem anatomy with water flow. The median section yielded a lower conductance value for an interval (Table 1), although the variation within a typical rachis interval (about 1 cm) is small enough that any point along it would give a similar result. Within a given rachis interval, total calculated conductances for the two adaxial bundles remain fairly constant even though tracheid features and therefore hydraulic conductances in each bundle vary according to the departure of pinnal vasculature. The overall decrease in hydraulic conductance along the rachis is most strongly influenced by a decrease in the number and the diameters of the largest tracheids. In the uppermost rachis, there is relatively little xylem tissue and it is composed exclusively of extremely narrow tracheids.

Pressure bomb measurements of heterogeneous samples yield a value for water potential (neglecting apoplastic osmotic potential) reflecting the volumes and elastic moduli of each component tissue placed in the chamber. Root tip and pinnal water potentials were thus weighted averages for these regions. Root tip water potentials and soil water potentials were used to calculate the soil conductance, which is thus somewhat arbitrary. Using a single water potential within the relatively short rhizome to calculate both root and stipe conductances apportions the rhizome conductance between these two structures.

Estimates based on the Hagen-Poiseuille equation consistently overestimated K_h of roots, stipes, and rachis by a factor of about two. This nearly constant relationship supports the assumption that conduit number and diameter are the principal determinants of conductance in plants. Such agreement is not limited to xylary systems consisting of only tracheids. Factors of 1.5–3.0 were found for *Acer rubrum* (Tyree and Zimmermann, 1971), closely matching the data presented here. In other ferns, a range of 2.8 to 5.5 was obtained (Woodhouse and Nobel, 1982). Data from *Lycopersicon* showed a factor varying around 1 (Dimond, 1966). In another study (Giordano et al., 1978) Hagen-Poiseuille overestimates ranged from 2 to 100 for single xylem vessels, which caused these workers to conclude that the equation cannot be applied to flow in the xylem. In addition to the effects of pits and cell wall irregularities which could cause deviations from the Hagen-Poiseuille equation, another major difficulty is the estimation of the effective conducting area of a tracheid or vessel. Calculations based on the diameter of the largest circle that could fit within a tracheid ignore a portion of the lumen that would be conducting, while calculations based on the diameter of a circle of area equal to the actual tracheid area overestimate the effect of that portion. Using the larger diameter would here increase the calculated values of K_h by an average of 2.4 fold, underscoring the susceptibility of the calculation to systematic errors and to assumptions.

In summary, anatomical description and physiological analysis of xylem have shown general differences between ferns and seed plants, as well as a wide range among ferns (Woodhouse and Nobel, 1982). This report begins a more detailed survey of xylem structure and function in ferns, and demonstrates that our present understanding of how tracheid number and dimensions affect water flow is of utility, but requires further refinement. In accord with xylem conductances calculated from the Hagen-Poiseuille equation, the water potential gradient was quite constant along root, stipe, and rachis. The larger gradients along the pinnae can be accounted for by lower conductances of the petiolule and pinnal lamina, rather than a constricted zone in the xylem pathway or a very small conductance from xylem to sites of water evaporation within the lamina. Evaluation of conductances by combining measurements of small excised sections with those for intact plants will lead to a better understanding of the structure-function relations of the xylem of ferns in particular and plants in general.

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