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STIPE ANATOMY, WATER POTENTIALS, AND XYLEM CONDUCTANCES IN SEVEN SPECIES OF FERNS (FILICOPSIDA)[1]

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ABSTRACT

Anatomy and water relations were studied for the desert fern *Notholaena parryi,* as well as six other ferns representing three different orders which occupied xeric as well as mesic habitats. Tracheid number and diameter, and total xylem cross sectional area increased during leaf development for *N. parryi*; the whole plant conductance (volume flow of water through a stipe divided by the rhizome-to-leaf water potential drop) increased but tended to level off as the leaves matured. The reported occurrences of very steep water potential gradients (about 25 MPa m^{-1}) in stipes of *N. parryi* were confirmed. The ferns with the highest whole plant conductances (*Alsophila australis, Botrychium dissectum,* and *Adiantum capillus-veneris*) had the largest or greatest number of tracheids. Numerous tracheids in *Botrychium dissectum* offset a low tracheary conductivity, whereas *Marsilea vestita* had few tracheids resulting in a low whole plant conductance. Whole plant conductances for the ferns were 2 to 3 orders of magnitude less than those generally observed for angiosperms and 6 orders less than for gymnosperms. However, the relative conductivity (whole plant conductance times stipe xylem length divided by xylem area) was only 5- to 10-fold less than for angiosperms and about the same as for the gymnosperms. Stipe water relations in these ferns are discussed in relation to the evolution of xylem anatomy.

THE PHYSIOLOGICAL ECOLOGY of ferns has received little attention (Wagner, 1973; Carlquist, 1975). The few physiological studies have been mostly concerned with the growth and development of gametophytes, spore germination, and morphogenic responses (Dyer, 1979). Ecological studies have been mainly descriptive; e.g., Holttum (1954) described the ferns of Malaysia according to the conditions under which they grew. The limited gas exchange studies have often been concerned with sun/shade adaptation of the sporophyte (Böhning and Burnside, 1956; Hew and Wong, 1974; Friend, 1975; Ludlow and Wolf, 1975; Hariri and Prioul, 1978). Maximum rates and light saturation of photosynthesis have also been examined (see Ludlow and Wolf, 1975; Wong and Hew, 1976; Nobel, 1977). The interaction between physiology and microhabitat has apparently been extensively examined only for the desert fern, *Notholaena parryi* (Nobel, 1978).

Essentially, the only studies on fern water relations concern the effect of water stress on photosynthetic temperature optima and the measurement of stipe water potentials for *N. parryi* (Nobel, 1978; Nobel, Longstreth and Hartsock, 1978). Other anatomical investigations have, somewhat obliquely, provided information on fern water relations. In particular, the distribution and occurrence of tracheids and vessel elements (presumed to have greater conductivity) have been explored in the ferns and compared to other plant groups, and the implications of xylem and stem construction have been discussed (Carlquist, 1975). The present work on fern water relations developed from a previous observation of very high water potential gradients ($\Delta\Psi/\Delta x$) in stipes of *N. parryi* (Nobel, 1978). Anatomical and physiological parameters relating to water flow in the stipe xylem were examined for seven ferns from three orders and various habitats. These are discussed with respect to both ecological and evolutionary implications of fern water relations.

MATERIALS AND METHODS—*Botrychium dissectum* Spreng. var. *obliquum* (Muhl.) Clute (Order Ophioglossales) has a solitary, bipinnate leaf (frond) up to about 50 cm long and is generally found in woods or thickets of temperate North America. *Notholaena parryi* D.C. Eat. (Order Filicales) has tripinnate fronds up to 20 cm long and is found under overhanging rocks in the Sonoran and Mojave

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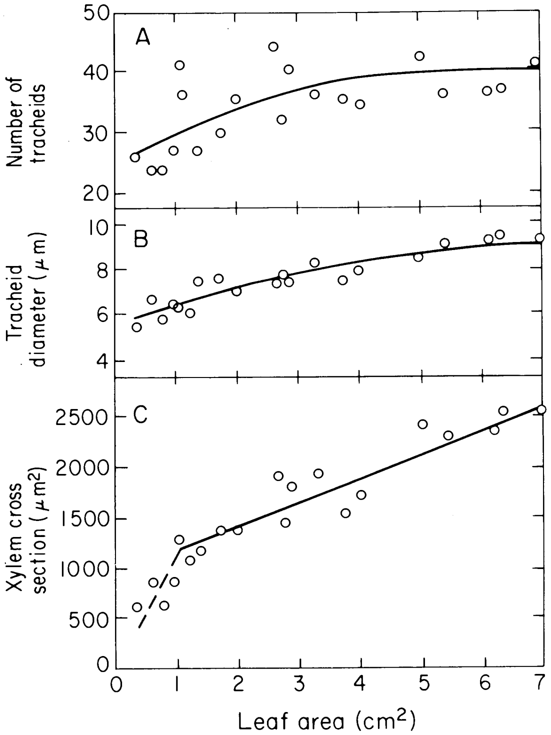

Fig. 1. Developmental changes in stipe anatomy for *Notholaena parryi*. The number (A), mean diameter (B), and xylem cross sectional area (C) were determined from individual stipes. Cross sectional area was determined from $\sum^{n} \pi d_i/4$, where d_i is the diameter of the i^{th} tracheid and n is the total tracheid number. The indicated regression equations are $Y = 25.5 + 4.83X - 0.434X^2$ ($r^2 = 0.43$) for (A), $Y = 5.6 + 0.90X - 0.058X^2$ ($r^2 = 0.88$) for (B), and $Y = 975 + 233.6X$ ($r^2 = 0.87$) for (C).

deserts. *Notholaena californica* D.C. Eat. has tripinnate fronds up to 15 cm long and occurs in habitats similar to *N. parryi. Adiantum raddianum* Presl. cv. Pacific Maid (Order Filicales) has tripinnate fronds up to 25 cm long, whereas *Adiantum capillus-veneris* L. differs by having a longer rachis between pinnae resulting in a less condensed canopy. Both species have warm-temperate and tropical distributions and are found in rock crevices and moist shaded seeps. *Alsophila australis* R.Br. (Order Filicales) is a tree fern with a trunk up to 8 m high and 13 cm in diameter and has tripinnate fronds that can be over 1 m in length; it is subtropical, centered in southeastern Australia. *Marsilea vestita* Hook and Grev. (Order Marsileales) has a quadripartite frond on petioles (stipes) up to 35 cm tall and is found across temperate North America in seasonally aquatic habitats as well as in tropical regions. Species of *Notholaena* and *Adiantum capillus-veneris* were collected at the Philip L. Boyd Deep Canyon Desert Research Center, Palm Desert, CA, whereas the other species were obtained from commercial sources.

Plants were maintained in a growth chamber with a 12-hr day at 27 C, a 21-C night, and an air water vapor concentration of about 13 g m^{-3}. Fluorescent (Sylvania Vita Lite 96T12 HO 800 ma) and incandescent (GE 60 W) lighting supplied 200 μmol m^{-2} s^{-1} of photosynthetically active radiation at the leaf surfaces (9% from the incandescents). Plants from the Deep Canyon Research Center were transplanted in native soil, and the others were grown in 1:1:2 sandy soil : peat moss : Vermiculite. All plants were watered every 2–3 days with one-fifth Hoagland's solution. Fronds used for analysis developed under chamber conditions. Anatomical and physiological comparisons of chamber and field grown fronds did not reveal significant differences.

Leaf conductance for water vapor loss was determined using a Lambda Instruments LI-60 diffusive resistance porometer with an LI-20S sensor that was calibrated before and after each use. Values for each side of the frond were added to give the overall leaf water vapor conductance (g_{wv}). When fronds did not fully cover the sensor aperture, proportional corrections were made based on the actual frond area exposed to the water vapor sensor. Frond area was determined with a Lambda Instruments LI-3000 portable area meter. Water potentials (Ψ in MPa, where 1 MPa = 10^6 N m^{-3} = 10 bars) of the stipe xylem were measured with a PMS Instruments 1000 Scholander-type pressure bomb. Stipes were severed as close as possible to the first pinna for the Ψ_{apex}^{stipe} measurements (placing the frond in the pressure bomb; Nobel, 1978) and as close as possible to the rhizome for Ψ_{base}^{stipe} measurements (placing the rhizome in the pressure bomb). Tracheid number and lumen diameter were determined from drawings of thin freehand sections of fern stipes rendered at 400× using a camera lucida and stage micrometer attached to a Zeiss phase contrast research microscope. Stipes from each fern species were initially sectioned at several places to determine whether anatomical changes occurred along the stipe, subsequent sectioning being performed for representative locations near the middle of the stipe.

Xylem conductance analysis was based on definitions from Hellkvist, Richards and Jarvis (1974). The whole plant conductance (K_{wp}) to

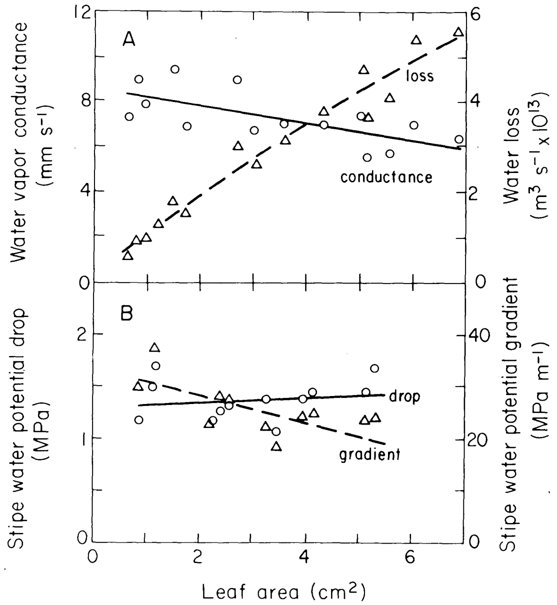

Fig. 2. Developmental changes in stipe water relations for *Notholaena parryi*. To determine total water loss (q) for individual stipes (A), g_{wv} was multiplied by the leaf-to-air water vapor concentration drop and leaf area. The stipe water potential drop ($\Psi_{apex}^{stipe} - \Psi_{base}^{stipe}$) was divided by stipe length to obtain the stipe water potential gradient (B). The indicated regression equations are $Y = 8.6 - 0.44X + 0.012X^2$ ($r^2 = 0.45$) for g_{wv}, $Y = 1.6 + 9.38X - 0.241X^2$ ($r^2 = 0.96$) for q, $Y = 1.23 + 0.026X$ ($r^2 = 0.04$) for stipe water potential drop, and $Y = 31.9 - 2.54X$ ($r^2 = 0.45$) for stipe water potential gradient.

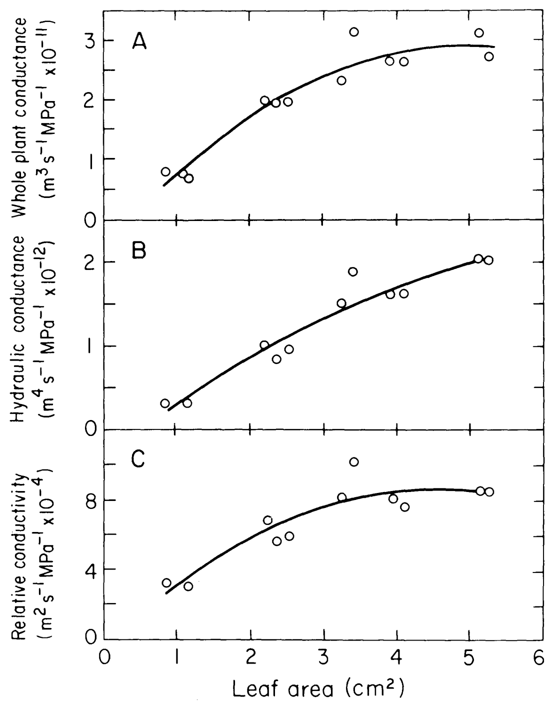

Fig. 3. Whole plant conductance (A), stipe hydraulic conductance (B), and relative conductivity (C) were calculated for fronds of *Notholaena parryi* of various leaf areas using data in Fig. 2. The indicated regression equations are $Y = -0.047 + 0.136X - 0.0137X^2$ ($r^2 = 0.93$) for (A), $Y = -0.36 + 0.70X - 0.046X^2$ ($r^2 = 0.93$) for (B), and $Y = -0.3 + 3.9X - 0.425X^2$ ($r^2 = 0.84$) for (C).

water flow is the volume flow of xylem sap up the stipe (q in m^3 s^{-1}) divided by the water potential drop from the rhizome to the pinnae ($\Psi_{apex}^{stipe} - \Psi_{base}^{stipe}$); q was calculated from g_{wv} and leaf area. Stipe hydraulic conductance per unit length (K_h) was q divided by the stipe water potential gradient ($\Delta\Psi/\Delta x$). Relative conductivity (K_{rel}) equaled K_h divided by the cross sectional area of the conducting tissue.

RESULTS—Tracheid number increased from about 22 to 40 and diameter from 5.5 to 9.0 μm as leaf area increased from 0.5 to 7 cm^2 for *Notholaena parryi* (Fig. 1A and 1B). Xylem cross sectional area doubled as leaf area increased from 0.5 to 1.0 cm^2 and doubled again by 7 cm^2 (Fig. 1C). For this 14-fold increase in leaf area, g_{wv} decreased about 30% and so total water loss per stipe increased just over 10-fold (Fig. 2A). The water potential drop along the stipes remained at about 1.2 MPa during leaf development, but the gradients decreased about 40% (Fig. 2B), since the stipes increased in length from 5 to 8 cm. All the measures of stipe conductance and conductivity increased as the leaf area increased (Fig. 3), which led to the above-mentioned increase in water flow (q) as the leaves developed.

Table 1 compares the seven species of ferns considered here. The tree fern *Alsophila australis* had the greatest leaf area per stipe, *Adiantum raddianum* and *A. capillus-veneris* were intermediate, and the other species had a considerably smaller leaf area. Tracheid number was about 5-fold higher for *Botrychium dissectum* and *Alsophila australis* compared to the other five species (Table 1), while *A. australis* had the largest average tracheid diameter followed by *Adiantum capillus-veneris*. The desert ferns (*Notholaena parryi* and *N. californica*) had the highest average g_{wv}. The average stipe water potential drop was lowest for *Botrychium dissectum* (0.7 MPa) and *Alsophila australis* (0.8 MPa) and highest for *Marsilea vestita* (2.4 MPa). The desert ferns had the greatest stipe water potential gradients, about 25 MPa m^{-1}, reflecting in part their high g_{wv}. K_{wp} was about 100-fold higher

TABLE 1. *Summary of anatomical and water relations parameters for seven fern species. Values indicated are means followed by standard deviations for at least 10 measurements along a developmental sequence* (cf., Fig. 1–3)

	Botrychium dissectum	*Notholaena parryi*	*Notholaena californica*	*Adiantum raddianum*	*Adiantum capillus-veneris*	*Alsophila australis*	*Marsilea vestita*
Leaf area (cm^2)	9.0 ± 2.9	3.3 ± 2.1	4.4 ± 3.6	25.7 ± 19.0	31.5 ± 27.5	213 ± 225	7.0 ± 6.6
Tracheid no.	190 ± 47	34.8 ± 5.8	34.0 ± 12.4	27.7 ± 5.7	33.0 ± 11.0	228 ± 195	40.9 ± 19.0
Tracheid diam (μm)	9.7 ± 0.3	7.9 ± 1.3	10.2 ± 0.8	10.0 ± 1.5	15.4 ± 2.4	18.9 ± 3.9	10.5 ± 2.6
Stomatal conductance ($mm\ s^{-1}$)	2.8 ± 0.8	7.4 ± 1.1	6.3 ± 1.0	1.6 ± 0.4	3.4 ± 0.6	4.1 ± 0.1	3.8 ± 1.2
Stipe water potential drop (MPa)	0.7 ± 0.1	1.3 ± 0.2	1.1 ± 0.2	1.1 ± 0.1	1.0 ± 0.2	0.8 ± 0.2	2.4 ± 0.6
Water potential gradient ($MPa\ m^{-1}$)	11.7 ± 3.9	24.0 ± 5.5	24.6 ± 9.8	14.0 ± 7.5	10.8 ± 4.5	2.3 ± 0.5	20.7 ± 3.7
Whole plant conductance ($m^3\ s^{-1}\ MPa^{-1} \times 10^{-11}$)	5.9 ± 1.5	2.1 ± 1.2	4.1 ± 2.9	5.5 ± 3.6	6.3 ± 3.7	136 ± 88	1.8 ± 1.0
Stipe hydraulic conductance ($m^4\ s^{-1}\ MPa^{-1} \times 10^{-12}$)	3.4 ± 1.2	1.3 ± 0.6	1.9 ± 1.8	3.0 ± 2.9	5.9 ± 5.5	452 ± 350	2.1 ± 1.2
Relative conductivity ($m^2\ s^{-1}\ MPa^{-1} \times 10^{-4}$)	2.3 ± 0.7	6.9 ± 2.2	6.4 ± 3.3	13.9 ± 10.3	9.6 ± 5.8	67.5 ± 11.9	6.0 ± 1.3

for *Alsophila australis* than for *Notholaena parryi* and *Marsilea vestita.* Also, K_h was about 100-fold higher and K_{rel} 10-fold higher for *Alsophila australis* than the other six species (Table 1).

DISCUSSION—The ferns examined here tended to have fairly typical leaf water vapor conductances but smaller diameters for the conducting elements of the xylem and hence higher water potential gradients than other plants. The values of g_{wv} for *Notholaena parryi, Adiantum raddianum,* and *Alsophila australis* are similar to previous observations on these species (Nobel, 1977; Nobel et al., 1978) but generally higher than for other ferns such as *Pteridium aquilinum* and *Pyrrosia longifolia* (Gates, 1968; Wong and Hew, 1976). The desert ferns *Notholaena parryi* and *N. californica* had values of g_{wv} that were nearly twice those of the five other ferns examined; this would facilitate rapid CO_2 uptake when water is available. This may represent an important adaptation to desert conditions, since the fronds are ephemeral and dry rapidly when soil moisture decreases, which frequently occurs in the desert. The average diameter of tracheids for the ferns investigated here is 3 to 15 times less than for ring-porous dicotyledonous trees, up to 8 times less than for diffuse porous dicotyledonous trees, up to 2 times less than for conifers (Zimmermann and Brown, 1971), but similar to those of some herbaceous dicotyledons (Jeje and Zimmermann, 1979). The drop in potential along the xylem of ferns is similar to values found for conifers and dicotyledons (Janes, 1970; Hellkvist et al., 1974). However, because most of the ferns have fairly short stipes, large gradients are developed (Table 1), in agreement with previously reported values for *N. parryi* (Nobel, 1978). In fact, all the ferns examined except *Alsophila australis* (which had many relatively large tracheids) had a gradient that was generally 10-fold higher than maximum values and several orders of magnitude greater than typical values for gymnosperm and angiosperm stems (Zimmermann and Brown, 1971; Jarvis, 1975).

The Hagen-Poiseuille law can be used to relate the pressure potential gradient ($\Delta P/\Delta x$) to the anatomy of the xylem and q (water loss):

$$\frac{\Delta P}{\Delta x} = \frac{128\eta q}{\pi \sum^{n} d_i^4}$$

where η is the viscosity of water, n is the number of tracheids, and d_i is the diameter of the i^{th} tracheid (Nobel, 1974). The equation is based on ideal, long, horizontal, constant-diameter tubes and often underestimates the gradient because of deviations of real systems from the necessary assumptions, but it does indicate the important influence of tracheid number and especially diameter (Zimmermann and Brown, 1971; Giordano et al., 1978; Petty, 1978). Correcting $\Delta\Psi/\Delta x$ for the static vertical gravitational gradient ($0.01\ MPa\ m^{-1}$), the calculated $\Delta P/\Delta x$ ranged from 36% of the measured value for *Adiantum raddianum* and *Notholaena parryi* to 18% for *Botrychium dissectum.* Although predicting quite large $\Delta P/\Delta x$ for fern stipes, the Hagen-Poiseuille law thus underestimated gradients by 3- to 5-fold, which is similar to underestimates for dicotyledons

(Zimmermann and Brown, 1971). In ferns the underestimate probably reflects the nonuniform walls and the pit connections of the imperforate tracheids, which are not accounted for in the ideal-case equation (Zimmermann and Brown, 1971).

The values of stipe conductances (K_{wp}, K_h, and K_{rel}) for *Alsophila australis* are consistent with its many relatively large tracheids, which support a considerable leaf surface area. The high stipe conductance may contribute to the limited habitat of *A. australis,* which like dicotyledonous trees with vessel-less xylem is restricted to mesic situations (Carlquist, 1975). Both *Botrychium dissectum* and *Adiantum capillus-veneris* have moderate K_{wp}'s and occur in slightly drier temperate habitats. The greater K_{wp} for *A. capillus-veneris* is mainly due to its larger tracheids than for *A. raddianum.* The low K_{rel} (which reflects properties of individual tracheids) for *Botrychium dissectum* is offset by a large number of tracheids, leading to the moderate K_{wp} for this species. A low K_{wp} limits water movement to the fronds, which may be advantageous for ferns exposed to drought. Hence, the low K_{wp} of *Marsilea vestita* is consistent with its ecological situation, where it functions as a xerophyte for long periods (White, 1963). The desert fern *Notholaena parryi* also has a low K_{wp}, but another desert species, *N. californica,* has a K_{wp} about twice that of the former two ferns (Table 1). Here the higher K_{wp} may indicate the necessity for a wetter microhabitat for *N. californica* than for *N. parryi,* which may contribute to its highly restricted range (Tryon, 1956). The K_p of *N. parryi* increased as leaves expanded and then became essentially constant, reflecting developmental changes in xylem anatomy.

Except for *Alsophila australis,* K_{wp} and K_h for ferns are 2 to 3 orders of magnitude less than for dicotyledons and 6 orders less than for conifers (Hellkvist et al., 1974). Values for *A. australis* are at the low end of the range for dicotyledons. The very large difference in K_{wp} and K_h between these groups is because ferns do not develop secondary xylary tissue nor do they have a large ring of conducting tissue as is found in conifers. Although there is a great deal of overlap among groups, imperforate tracheary elements underwent phylogenetic modification in the angiosperms by becoming shorter and fatter with modified pit fields (Esau, 1965), contributing to greatly increased values for K_{wp} and K_h. K_{rel} for ferns is similar to conifer values, 5-fold less than for diffuse-porous deciduous dicotyledonous trees, and 10-fold less than for ring-porous deciduous trees and herbaceous dicotyledons (Heine, 1971; Hellkvist et al., 1974). Since fern and conifer tracheids are similar (Esau, 1965), a similar K_{rel} for both groups is reasonable. The relative primitiveness of tracheids, coupled with their low numbers and small diameters for most ferns, restricts these species to being rather short or slow growing.

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No. 9, October (Article by Brown and Clark), pages 1218–1221. The first published chromosome count for *Haplopappus glutinosus* is not ours (Brown & Clark) but instead needs to be credited to:

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