

**INFLUENCE OF PLANT SIZE ON THE ECOPHYSIOLOGY OF THE
 EPIPHYTIC FERN *ASPLENIUM AURITUM* (ASPLENIACEAE)
 FROM COSTA RICA¹**

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- *Premise of the study:* A central goal of plant ecophysiological studies is to generate patterns of physiological behavior that are applicable to a species, which can be complicated when plant size is considered. Studies indicate that plant size can influence numerous ecophysiological parameters, especially in vascular epiphytes. The few studies that have included ferns in their analyses suggest that plant size is less important in ferns than angiosperms. This study investigates this apparent disparity by examining the relationship between plant size and an array of ecophysiological parameters in the epiphytic fern *Asplenium auritum*, especially the role of plant size in determining responses to water stress.
- *Methods:* Plants were classified according to size and measured for a variety of functional traits, including maximum photosynthetic rate, stomatal conductance, water-use efficiency, stomatal density, chlorophyll content, chlorophyll *ab* ratio, specific leaf area, whole plant drying rates, and desiccation tolerance. Results for all traits were compared across size classes to determine size-related differences.
- *Key results:* Plant size significantly influenced most traits examined, most notably photosynthetic rate, stomatal density, stomatal conductance, whole plant drying rates, and recovery from desiccation. We report the first evidence of size-mediated shifts in desiccation tolerance in plants: small individuals tolerated water loss, whereas larger individuals avoided desiccation.
- *Conclusions:* Our findings indicate that size-mediated ecophysiological shifts are more important than previously thought in ferns, particularly in regard to water relations. Desiccation tolerance may allow young fern sporophytes to establish in stressful environments and is subsequently lost in older individuals.

Key words: *Aspleniaceae; Asplenium auritum;* desiccation tolerance; ecophysiology; fern; photosynthesis; plant size.

A central goal of plant ecophysiological studies is to generate patterns of physiological behavior that are widely applicable to a given species. Fulfilling this goal can be complicated when aspects of plant size are considered. A number of studies indicate that plant size may significantly influence ecophysiological parameters, particularly those pertaining to photosynthetic capacity and nutrient relations (Kull and Koppel, 1987; Zotz and Winter, 1994; Zotz, 1997; Schmidt et al., 2001; Schmidt and Zotz, 2001; Zotz et al., 2001, 2002, 2011; Martin et al., 2004; Ishida et al., 2005; Cavallero et al., 2009; Lorenzo et al., 2010). Schmidt et al. (2001) investigated the relationship between plant size and several photosynthetic variables in 10 species of epiphytes from a tropical lowland forest in Panama. They reported that more variation was found between different sized plants of the same species than between similarly sized plants of different species for several physiological traits. In a study examining the influence of plant size on nutrient relations, Reich et al. (2003) found that epiphytic bromeliads undergo radical shifts in nitrogen relations as they increase in size. Small

individuals received 64–72% of their nitrogen from atmospheric sources while large individuals could receive up to 100% of their nitrogen from soil-derived sources. These findings indicate that understanding the role that plant size plays in determining the physiological behavior for a given species is a crucial not only for understanding factors controlling its ecology and distribution at local and regional scales, but also to determine how to best sample that species. As such, evaluating plant size in an ecophysiological context is a potentially important and often overlooked prerequisite of plant ecological inquiry.

The majority of studies on plant size have been limited to trees (Kull and Koppel, 1987; Cavaleri et al., 2010; Coopman et al., 2011; Osada, 2011; Sterck and Schieving, 2011) and epiphytic angiosperms such as bromeliads and orchids (Zotz and Ziegler, 1999; Schmidt et al., 2001; Zotz et al., 2011). Despite their significant contribution to many floras, particularly tropical forests, ferns have been seriously underrepresented in these studies. Unlike other studies on seed plants, a detailed study on the old-world bird's nest fern, *Asplenium nidus* L., found little evidence for size-related impacts on physiology (Martin et al., 2004). This study found no significant relationship between plant size and frond conductance to CO₂ or the internal CO₂ concentration of the fronds. When mineral relations were examined, they found strong relationships between some micronutrients and size but no significant relationship between N and P. Schmidt et al. (2001) examined a number of epiphytic plant species and found somewhat stronger links between size and physiology in the neotropical epiphytic fern *Niphidium crassifolium* (L.) D. B. Lellinger. In this species both leaf N content

¹Manuscript received 1 July 2012; revision accepted 10 October 2012.

The authors thank Gerhard Zotz and an anonymous reviewer for insightful and thorough comments that greatly improved this manuscript. The authors thank Catherine Cardelús for helpful comments on an earlier version of the manuscript.

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and photosynthetic capacity were tied to plant size, yet when compared across nine species, *N. crassifolium* had the second lowest deviation of photosynthesis with size. With so few studies available, the data for ferns are ambiguous. Could these differences be driven by physiological limitations resulting from inefficient stomatal control (Brodribb and McAdam, 2011; McAdam and Brodribb, 2012) and highly resistive, tracheid-based vasculature (Watkins et al., 2010) or have simply too few species been sampled?

Epiphytes seem to be particularly subject to size-dependent physiological impacts. Given that epiphytes are physically disconnected from large water and nutrient pools, they are subject to a number of unique stresses relative to terrestrial species (Cardelús et al., 2009; Watkins and Cardelús, 2009). A few unusual species, many of which are epiphytes, have developed desiccation tolerance: the ability to dry into equilibrium with their surrounding air and recover (Pessin, 1925; Stuart, 1968; Bewley, 1979; Reynolds and Bewley, 1993; Alpert, 2000; Oliver et al., 2000; Proctor and Tuba, 2002; Watkins et al., 2007; Hietz, 2010). In the plant kingdom desiccation tolerance is rare; ~0.1% of modern flowering plants exhibit desiccation tolerance in their vegetative tissues (Alpert, 2000). The ability to tolerate desiccation seems to impose a size limit on plants with the character apparently limited to relatively small plants (Bewley, 1979, Oliver et al., 2000). Little work has been done to examine the influence of intraspecific plant size on desiccation tolerance.

This paper describes the influence of plant size on the ecophysiology of *Asplenium auritum* Sw., a medium-sized epiphytic fern that is widely distributed in neotropical wet forests (Moran and Riba, 1995). This species was selected for this study because of its broad distribution, epiphytic habit, considerable size variation, and gross morphology, which is more typical of many tropical fern species than other taxa previously studied (e.g., *A. nidus*). These characteristics make this species an exceptional model for better understanding the link between plant size and ecophysiological behavior in ferns as well as inferring potential ecological consequences of such a relationship. We hypothesized that plant size would strongly influence a number of ecophysiological traits, with larger plants exhibiting, most notably, higher photosynthetic rates, higher stomatal conductance, slower drying rates, and reduced desiccation tolerance compared to smaller individuals.

MATERIALS AND METHODS

Study site—This study was conducted over the course of two consecutive summers, 14 June 2010 to 1 July 2010 and 27 June 2011 to 14 July 2011 at La Selva Biological Station (Heredia Province) in the Atlantic lowlands of northeastern Costa Rica (10°25.591'N, 084°00.37'W). This station contains 1400 ha of tropical wet forest with a mean annual rainfall total of ~4000 mm (Cardelús et al., 2009). Precipitation peaks in June or July and November or December, but mean monthly rainfall is never below 150 mm·mo⁻¹. This study was conducted on the border of secondary forest and an open field, and all plants were collected between 0 and 2.5 m above the ground on trees ranging from 0.9 to 1.8 m DBH. Mean daily air water potentials (\pm SE) ranged from $-5 (\pm 4)$ MPa in the early morning and evening to $-37 (\pm 9)$ MPa in the midafternoon (Fig. 1). Mean midday irradiance (photosynthetically active radiation; PAR) ranged from 5 to 30 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at positions along tree trunks where the ferns were growing.

Study species—*Asplenium auritum* (Aspleniaceae) is a small to medium-sized epiphyte that is common in secondary forests at La Selva. The species occurs in a wide variety of environments, but is always found either epiphytically

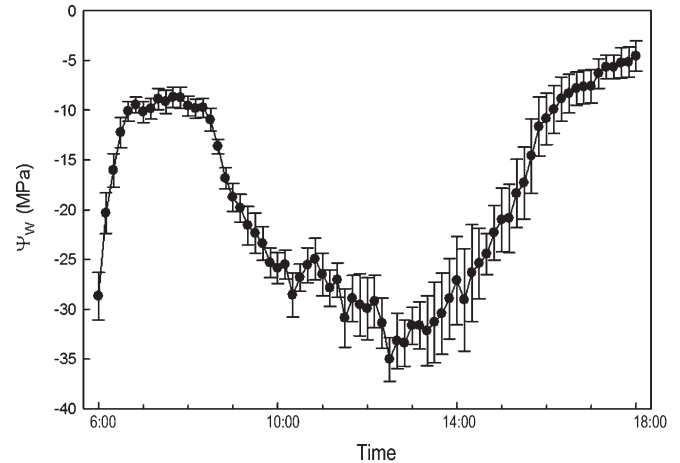


Fig. 1. Mean daily water potential values at study site as recorded by four climate data loggers placed among study populations of *Asplenium auritum* between 21 and 27 June 2010. Error bars represent ± 1 SE ($N = 4$).

or epipetrically. The species frequently colonizes trees along field edges forming populations of several hundred mixed sized individuals. No capacity for sporophytic asexual reproduction is known in this species; gametophytes display indeterminate growth typical of epiphytic species. Individual plants used in all experiments were classified into one of three size classes according to the length of their longest frond: small (>10 cm), medium (10–20 cm) and large (<20 cm) (Fig. 2). This classification was used because individuals within these populations could easily be grouped into these classes, and each size class was well represented within the population. Sterile fronds were selected for all measurements to eliminate physiological or morphological differences that may be due to the presence of reproductive organs, the sori.

Frond morphology—Twelve plants from each size class were collected for frond morphology measurements, including length of longest frond, total leaf area (TLA), specific leaf area (SLA), and stomatal density. Total leaf area of live tissue of each plant was measured with a Li-Cor 3100C area meter (Li-Cor BioSciences, Lincoln, Nebraska, USA). We measured SLA ($\text{g}\cdot\text{cm}^{-2}$) by punching 10 holes (0.1 cm^2 area) in one pinna per plant, drying the tissue at 60°C for 72 h followed by weighing the tissue. To control for foliar variation, we selected pinnae from the middle 1/3 of the frond and took punches from between the midrib and pinnule margin. Stomatal density was determined by viewing impressions made with clear nail polish under a Nikon Optiphot 2 light microscope (Nikon Instruments, Melville, New York, USA) at 40 \times magnification and calculating mean density. Two impressions between secondary veins were used per plant.

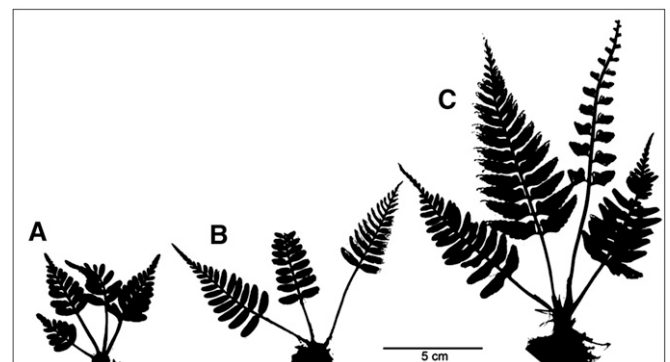


Fig. 2. Silhouettes of (A) small, (B) medium, and (C) large plants of *Asplenium auritum* demonstrating size differences across size classes designated in this study.

Chlorophyll extraction—Leaf samples from five plants per size class were collected and extracted in *N,N*-dimethylformamide (DMF), and chlorophyll content per mass and chlorophyll *a/b* ratios were determined following the protocol of Moran (1982). Chlorophyll concentrations were determined using a Helios Beta Spectrophotometer, (Thermo Scientific, Waltham, Massachusetts, USA)

Drying/rehydration experiment—An additional 12 plants from each size class were carefully removed from the trunks of trees, cleaned thoroughly to remove all dirt and debris, and placed in sealed clear plastic chambers with moist paper towels for 24 h to allow for full hydration. Following this hydration period, dark-adapted photochemical efficiency (F_v/F_m) values were determined using a Walz Mini-PAM fluorometer (Heinz Walz, Effeltrich, Germany). Fresh masses were recorded, and plants were then placed in humidity-regulated chambers over a saturated solution of NaCl, which maintained constant water potential within the chamber of -38 MPa, as described by Greenspan (1977).

Following placement within the chambers, plants were weighed at 15, 20, 40, 60, 80, 100, 120, 150, 180, 210, 240, 270 and 300 min and then every subsequent 10 h until all plants had dried to equilibrium with the air within the chambers. After drying was complete, plants remained in the chambers for 48 h, then placed on trays and covered with moist paper towels to allow for rehydration. To determine plant recovery, we recorded F_v/F_m values of all plants were recorded at 5, 15, 30, 45, 60, 1440, and 2880 min post-rehydration. Following rehydration, total leaf area was determined, and plants were placed in a drying oven at 60°C for 48 h and weighed to determine dry mass, initial water content, relative water content (RWC), and nutrient contents (discussed below).

In situ gas exchange—To determine maximum photosynthetic rate, stomatal conductance, and water-use efficiency, we measured 10 plants per size class using a LI-6400 portable photosynthesis system (Li-Cor) in situ. Ambient light measurements were recorded at the position of the leaf being measured using the PAR sensor on the LI-6400 portable photosynthesis system. Gas exchange measurements were recorded at CO_2 concentration of $400 \mu\text{mol}\cdot\text{mol}^{-1}$ and $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR. Plants were exposed to these conditions for 420 s before measurement to allow for photosynthetic parameters to stabilize. Preliminary trials indicated that the light conditions and acclimatization times used were sufficient to allow plants to achieve maximum assimilation rates and for other photosynthetic variables to stabilize. Because most fronds did not completely cover the area within the measurement cuvette, the area of each measured leaf section was determined by scanning the frond and using the “analyze particles” tool in ImageJ image analyzing software (National Institutes of Health, Bethesda, Maryland, USA).

Leaf elemental analysis—For determination of leaf nitrogen content, tissue samples were excised from fronds used in gas exchange measurements and dried at 60°C for 48 h. Dried samples were then ground into a fine powder using a Wiley Mill (Thomas Scientific, Swedesboro, New Jersey, USA) and passed through a #40 screen. Samples were then rolled and combusted on a Costech CN analyzer (Valencia, California, USA) at Colgate University.

Statistics—One-way ANOVA followed by post hoc Tukey tests were run to determine differences between size classes for each variable measured. Total leaf area and maximum photosynthetic rate were regressed against maximum frond length using a generalized linear regression model. For all analyses, a significance level of 0.05 was used. All statistics were completed using the program JMP ver. 9.0.0 (SAS Institute, Cary, North Carolina, USA).

RESULTS

We surveyed plants of *A. auritum* across a range of sizes represented in the populations studied, with frond lengths from 3.2 to 40.3 cm. Total leaf area was strongly and positively correlated with maximum frond length (Fig. 3, $R^2 = 0.884$, $P < 0.001$), indicating that maximum frond length was an effective predictor of overall plant size. The other leaf morphology traits examined varied across size classes as well. Both stomatal density and SLA were significantly higher in small plants than medium and large plants (Fig. 4A, Table 1).

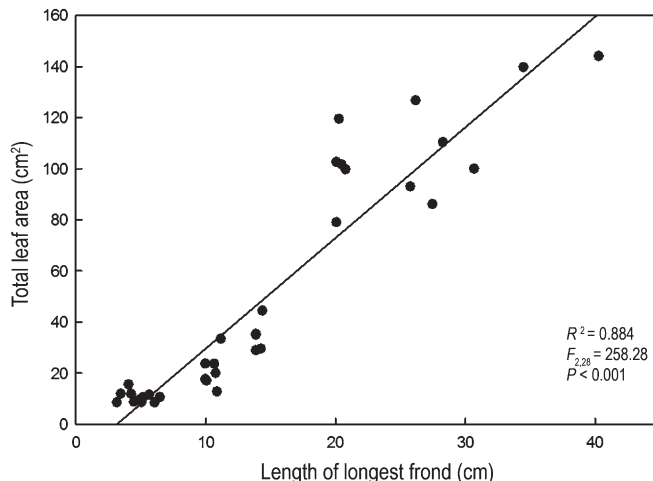


Fig. 3. Plot of linear regression analysis showing relationship of total leaf area (TLA) with maximum frond length in *Asplenium auritum*. $R^2 = 0.884$, $F_{2,28} = 258.28$, $P < 0.0001$.

Some, but not all water relations variables varied across size classes. Total initial water content was significantly lower in large plants than in medium and small plants (Table 1). Smaller plants dried faster than both medium and large plants (Fig. 5), with small plants drying to 50% RWC after ~ 300 min compared to a mean of ~ 1800 min for large individuals. Mean post-desiccation values of RWC did not vary significantly across size classes (Table 1, $F_{2,33} = 0.910$, $P = 0.416$). Rates of post-rehydration recovery of photochemical efficiency also varied significantly across size classes, with small and medium-sized plants recovering more quickly than large plants; at 48 h post-rehydration, mean percentage recovery of F_v/F_m remained lower in large plants than in medium or small plants (Fig. 6; Table 1, $F_{2,33} = 5.817$, $P = 0.007$).

Photosynthetic variables varied across size classes. Mean mass-based chlorophyll content was greater in large plants than in medium and small plants, though not significantly ($P = 0.075$); chlorophyll *a/b* ratios did not vary across size classes (Table 1). Maximum photosynthetic rate correlated positively with maximum frond length (Fig. 7, $R^2 = 0.516$, $P < 0.001$) and ANOVA analysis with post hoc Tukey tests resolved three homogeneous subsets coincident with each size class (Fig. 4B, $F_{2,27} = 22.316$, $P < 0.001$). Mean stomatal conductance of small plants was significantly lower than that of both medium and large plants (Table 1, $F_{2,27} = 5.709$, $P = 0.009$), while water-use efficiency (A_{\max}/g_w) did not differ significantly across size classes (Fig. 4C, $P = 0.112$). Leaf percentage nitrogen also did not differ significantly across size classes (Fig. 4D, $P = 0.183$).

DISCUSSION

This work complements the existing body of research on size-mediated ecophysiology of plants by providing a comprehensive investigation in the epiphytic fern *Asplenium auritum*. Prior work on many angiosperms (Franco et al., 1994; Desoyza et al., 1996; Cavender-Bares and Bazzaz, 2000; Zotz et al., 2001; Kubien et al., 2007) has demonstrated a strong link between plant size and nearly all traits examined, indicating that plant size—though generally ignored in studies of plant ecophysiology—should be

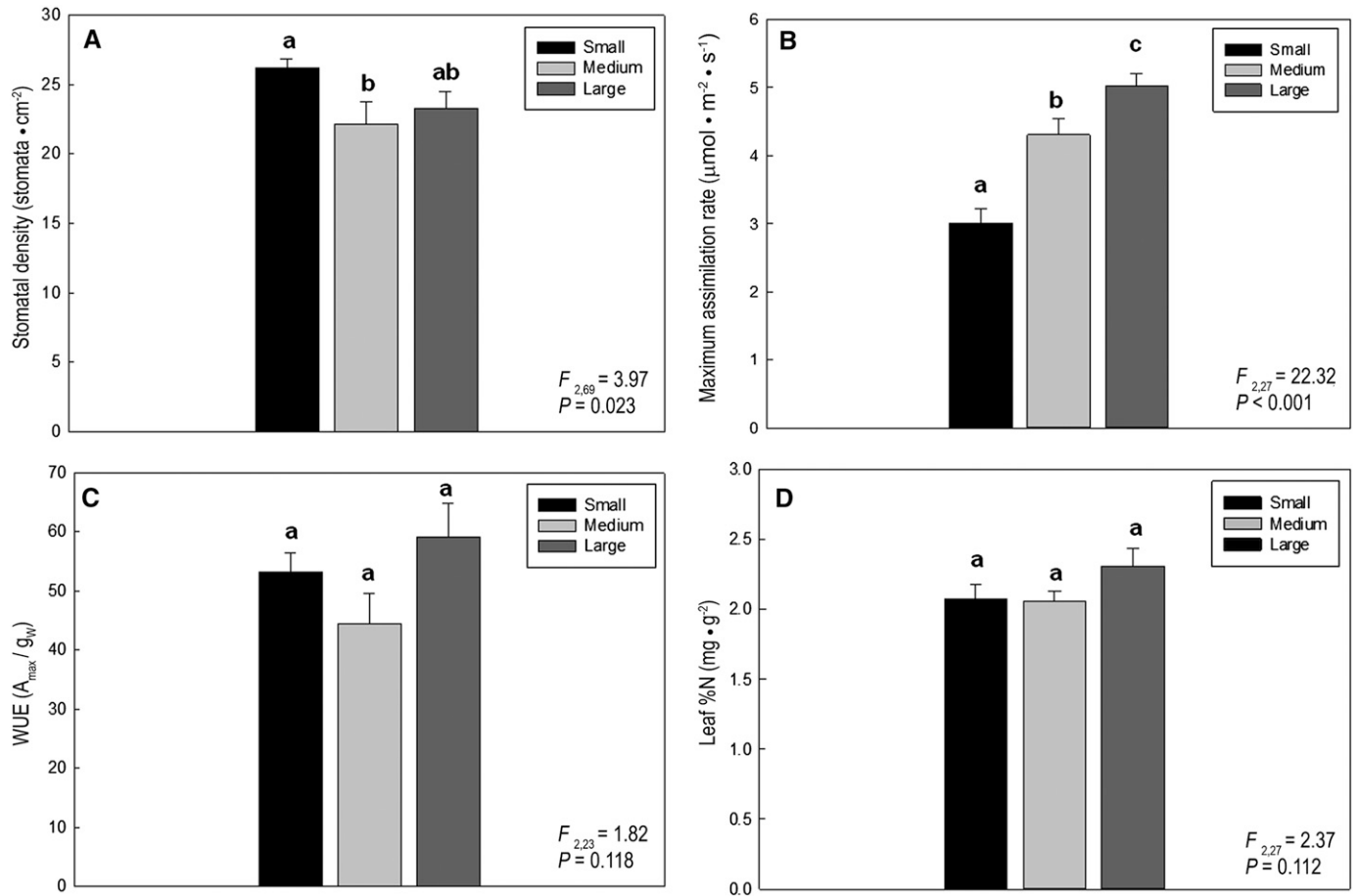


Fig. 4. Bar graphs comparing (A) stomatal density, (B) area-based photosynthetic rate, (C) intrinsic water-use efficiency, and (D) mass-based percent nitrogen. F - and P -values show results of one-way ANOVA. Lowercase letters denote homogenous subsets. Error bars represent ± 1 SE ($N = 24$ for A, $N = 12$ for B–D).

granted more attention. Vascular epiphytes seem particularly prone to physiological variation that closely corresponds to changes in plant size (Zotz et al., 2001). However, the nature of such relationships in other groups has been poorly explored, and questions remain as to how closely plant size is linked to physiology in groups like the ferns.

Unlike the Martin et al. (2004) study on the basket-forming epiphytic fern *Asplenium nidus*, our data indicate that there is a close relationship between many ecophysiological parameters

and fern size. In our study, stomatal density, SLA, initial water content, dry down rate, post-desiccation recovery, A_{\max} , and stomatal conductance all correlated with plant size.

While it is difficult to ascertain the causes underlying some of the observed trends, others are apparent and may have important functional significance. For example, the increased photosynthetic rates, decreased SLA, and higher chlorophyll content observed in large plants appear to be interrelated. Large plants had thicker leaves and increased chlorophyll content,

TABLE 1. Comparison of mean values of ecophysiological parameters of small, medium, and large plants of *Asplenium auritum*.

Trait	Small (SE)	Medium (SE)	Large (SE)	F (df)	P -value
Total leaf area (cm ²)	10.30 ^A (0.61)	26.65 ^B (2.68)	108.4 ^C (5.86)	197.665 _(2,28)	<0.001*
Specific leaf area (m ² ·kg ⁻¹ dried tissue)	20.68 ^A (1.02)	16.58 ^A (1.07)	14.29 ^B (0.60)	12.451 _(2,28)	<0.001*
Stomatal density (stomata·mm ⁻²)	26.23 ^A (0.61)	22.12 ^A (1.6)	22.48 ^B (1.2)	3.975 _(2,69)	0.023*
Chlorophyll content (μg Chl·mg tissue ⁻¹)	2.14 (0.18)	2.28 (0.13)	2.70 (0.17)	3.241 _(2,12)	0.075
Chlorophyll <i>a/b</i> ratio	0.89 (0.03)	0.93 (0.07)	0.89 (0.03)	0.319 _(2,12)	0.733
Initial water content (%)	75.32 ^A (0.94)	76.50 ^A (0.77)	72.24 ^B (0.45)	9.922 _(2,33)	<0.001*
Final water content (%)	12.62 (1.11)	14.14 (0.86)	12.90 (0.43)	0.910 _(2,33)	0.416
Percentage recovery of F_v/F_m at 48 h	96.36 ^A (1.53)	94.52 ^A (2.74)	86.51 ^B (2.15)	5.817 _(2,33)	0.007*
Maximum photosynthetic rate (μmol·m ⁻² ·s ⁻¹)	3.01 ^A (0.22)	4.31 ^B (0.24)	5.02 ^B (0.19)	22.316 _(2,27)	<0.001*
Stomatal conductance (mol·m ⁻² ·s ⁻¹)	0.058 ^A (0.005)	0.107 ^B (0.012)	0.096 ^B (0.014)	5.709 _(2,27)	0.009*
Water use efficiency (A_{\max}/g_i)	53.24 (3.21)	44.44 (5.08)	59.10 (5.72)	2.373 _(2,27)	0.112

Notes: Asterisks (*) denote statistically significant differences. Capital letters denote homogeneous subsets.

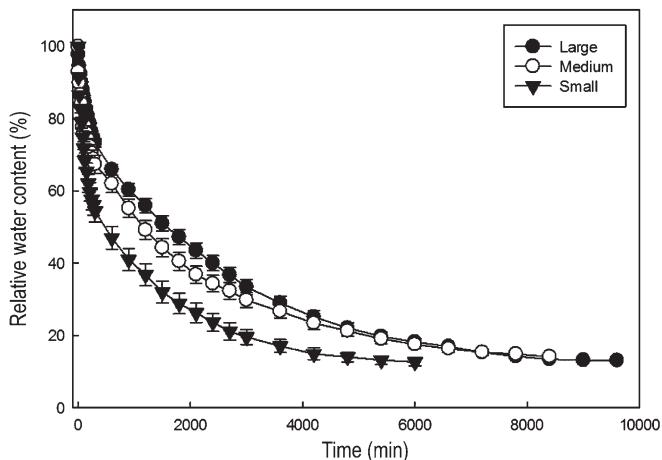


Fig. 5. Mean drying rates of small, medium, and large plants of *Asplenium auritum* when exposed to air water potential deficits of $\Psi = -38$ MPa in humidity-controlled drying chambers. Error bars represent ± 1 SE ($N = 12$).

consistent with our findings of increased maximum photosynthetic rates in the size class. The increased stomatal conductance observed in larger plants is certainly related to the trends observed in photosynthetic behavior and likely reflects the improved water status of larger plants during the day, at which time smaller individuals are partly desiccated. The higher stomatal density observed in small plants is likely related to their yet-incomplete leaf development; no difference was observed between mature plants in the medium and large size classes. The most remarkable size-trait relationships were those regarding water relations; these are discussed later.

These results are similar yet stronger than those reported for *Niphidium crassifolium* by Schmidt et al. (2001). Like *A. auritum*, *N. crassifolium* is incapable of forming a litter-trapping foliar arrangement and lacks the absorptive trichomes of *A. nidus*, suggesting that these two taxa may be functionally similar in

regard to nutrient and water relations. In their review of the topic, Zotz et al. (2001) suggest that water availability is the main driver behind size-mediated physiological changes. If this is the case, they argue that plants relying on internal stored water should exhibit a closer link with size than those that receive most of their water from external canopy soil. Thus, the relatively weak size link found in the Martin et al. (2004) study on *A. nidus* is surprising given that this species relies on stored water and recycled nutrients from decomposing organic material intercepted by their large leaves (Freiberg and Turton, 2007; Fayle et al., 2010). Additionally, many epiphytic ferns produce long creeping rhizomes that may be rooted in deep canopy soil along various sections. Potential increased capacitance, the ability to explore wetter soil pockets, and a disconnect between surface to volume ratio could reduce size-related shifts. *Asplenium auritum*, like *N. crassifolium*, does not produce significant creeping rhizomes, and the individuals in this study were not rooted in canopy soil. The stronger size-trait link observed in *A. auritum* may be due to the fact that individuals of this species are generally much smaller than *N. crassifolium*, thus limiting their ability to resist environmental fluctuations.

A disproportionate amount of attention in this field has been focused on epiphytic bromeliads, and it is unclear whether epiphytic fern species display similar ecophysiological behavior. Recent studies have shown that ferns may be less water use efficient than seed plants, resulting from inefficient stomatal control (Franks and Farquhar, 2007; Brodribb and McAdam, 2011; McAdam and Brodribb, 2012). Brodribb and McAdam (2011) and McAdam and Brodribb (2012) have shown that fern stomata rely on passive closure responding to leaf hydration status. Ferns may lack sophisticated mesophyll hormonal responses that are found in seed plants. Brodribb et al. (2005) have also argued that ferns rarely reach water potentials that would result in significant hydraulic failure from drought-induced cavitation. Low stomatal conductance, as exhibited by many fern taxa, may represent an important functional tradeoff: reduction of photosynthetic activity in order to maintain a safety threshold of water storage. However, these studies have focused almost entirely on mesophytic terrestrial species, and it is unclear

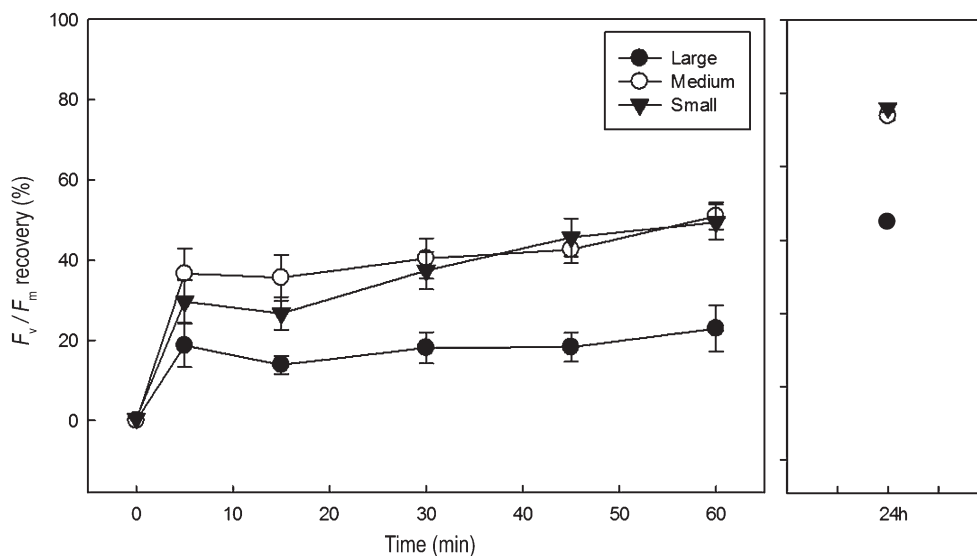


Fig. 6. Short-term post-rehydration recovery of photochemical efficiency, F_v/F_m , following 72-h exposure to water potential deficits of $\Psi = -38$ MPa in small, medium, and large plants of *Asplenium auritum*. Error bars represent ± 1 SE ($n = 12$).

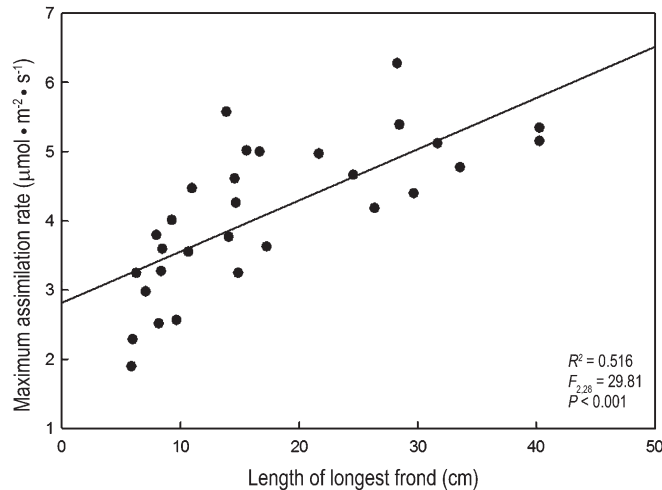


Fig. 7. Plot showing relationship of maximum photosynthetic rate (A_{\max}) and plant maximum frond length. $R^2 = 0.516$, $F_{2,28} = 29.814$, $P < 0.001$.

whether epiphytic species exhibit similar trends. More work needs to be done on water relations in ferns, especially with a focus on xerophytic species, before conclusive determinations of physiological limitations in the group can be made. Our findings suggest that some epiphytic ferns may possess far more sophisticated responses to water stress than is currently recognized.

To our knowledge, this is the first study demonstrating a link between plant size and desiccation tolerance. The dramatic shift in *A. auritum* from poikilohydry in small plants to a strategy of drought avoidance in larger individuals is particularly notable in the context of recent work on water relations in ferns. Small plants are more desiccation tolerant and can survive dry conditions and recover rapidly following periods of drought relative to larger individuals. However, constitutive production of metabolites associated with desiccation tolerance coupled with the cessation of metabolic activity during periods of drought makes desiccation tolerance a poor strategy for coping with water stress in competitive environments. Thus, it is apparently advantageous for larger individuals, which are able to avoid drought by means of a suite of morphological characters including increased frond thickness, reduced stomatal density, and thicker cuticles, tend to do so at the cost of reduced desiccation tolerance. It is unlikely that this reduced stress tolerance adversely affects large individuals; our results indicate that most daily dry-down events are both severe and long enough to cause small plants to dry to ~60% RWC, while large plants only dry to 80–85% RWC (Fig. 5). These differential drying rates seemingly necessitate desiccation tolerance by small plants, while larger individuals can continue to photosynthesize during periods of moderate water stress.

Similar abiotic conditions generate differential levels of stress on small and large plants. Thus, it seems likely that smaller plants more often experience moments of extreme desiccation and have adapted to this by becoming more desiccation tolerant. Fern gametophytes often demonstrate greater tolerance to both freezing and desiccation than sporophytes of the same species (Sato and Sakai, 1980; Farrar, 1998; Watkins et al., 2007); our findings suggest that similar variance in desiccation tolerance may occur across sporophyte size classes as well. Desiccation tolerance may be crucial in allowing establishment in stressful

environments; the presence of numerous fern taxa in these sites suggests that they may behave similarly to *A. auritum*. Further work is necessary to develop an understanding of the prevalence of such size-related physiological shifts and to provide a more comprehensive view of the importance of plant size in water relations.

Plant ecophysiologicalists are often interested in understanding patterns of physiological behavior that are widely applicable to a given species. Developing such patterns is especially difficult in vascular epiphytes that can have significant size-related physiological links. Understanding ontogenetic shifts in physiological response is critical to examination of species-level environmental integration. Without such studies, generating a synthetic understanding of organismal ecology and a species ability to adapt to a changing environment is obscured, and it is difficult to effectively assess physiological behavior within and across species. Our data are especially important in studies that consider the evolution of and ecological significance of plant tolerance to desiccation. Plasticity in desiccation tolerance is not well understood and the potential for size-mediated shifts in this tolerance will provide a novel window unto understanding how such an extreme adaptation has evolved and the ecological consequences of associated with it. If desiccation tolerance is more widespread than previously thought, it could serve as an important means by which ferns could overcome the physiological limitations poised by inefficient stomata and a tracheid-based vascular system and ultimately establish themselves as one of the dominant lineages of epiphytic plants.

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