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Effects of hydrology on the growth and physiology of an invasive exotic, *Lygodium microphyllum* (Old World climbing fern)

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Summary

We conducted a glasshouse study to examine effects of hydrology on the growth and physiology of *Lygodium microphyllum* (Old World climbing fern), an invasive exotic that is rapidly colonising forested wetlands in Florida, USA. We assessed the fern's growth and physiological responses to three hydrological treatments – flood, drought and field capacity. To further explore the physiology of the treatment responses of *L. microphyllum*, we also sprayed each plant with gibberellic acid, paclobutrazol (gibberellin inhibitor) or a water control solution (at a rate of 5 mL three times per week) using a 3×3 factorial design. Flooding reduced relative growth rate by 55%, whereas periodic exposure of ferns to a soil water potential of −1 MPa did not affect growth or physiology. Flooding led to substantial decreases in specific leaf area and area-based rates of pinna photosynthesis, resulting in a 64% lower rate of photosynthesis per unit pinna mass. Application of growth regulators had no effect on fern growth, morphology or physiology. Even though flooding substantially reduced growth, *L. microphyllum* still showed a positive relative growth rate after >2 months of inundated soils. This apparent hydrological plasticity is likely a contributing factor to the introduced fern's widespread establishment across a range of plant communities within the Florida Everglades ecosystem. Short-term manipulation of site hydrology does not appear to be an effective management option. Consequently, this has considerable implications for the Everglades, which is undergoing a 30-year system-wide hydrological restoration.

Keywords: relative growth rate, growth analysis, flooding, growth regulator, invasive species, alien, exotic species, gibberellic acid, paclobutrazol.

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Introduction

Colonisation of non-native habitats by invasive plant species can bring about a wide array of detrimental ecosystem perturbations, including altered ecosystem hydrology and biogeochemistry, disruptions of native flora and fauna and consequent losses in biodiversity (e.g. Vitousek *et al.*, 1997). In the contiguous United States, the Florida Everglades is one of the natural areas most affected by exotic invasive species (Schmitz *et al.*, 1997). Among the numerous invasive plant species found in the Everglades, the vine-like *Lygodium microphyllum* (Cav.) R. Br. (Old World climbing fern) poses one of the greatest threats, owing to its rapid spread and

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ability to dominate both the understory and overstory in native wetland habitats (Pemberton & Ferriter, 1998; Volin *et al.*, 2004). One of the fern's most destructive traits is its tendency to form dense rachis mats that can exceed 1 m in thickness, thus inhibiting the growth of native understory vegetation (Pemberton & Ferriter, 1998). The fern also climbs into the forest canopy, eventually collapsing canopy trees and/or altering local fire ecology through the formation of 'fire ladders' (Pemberton & Ferriter, 1998; Volin *et al.*, 2004).

According to a recent model developed by Volin *et al.* (2004), the landscape coverage of *L. microphyllum* infestations could exceed the current combined coverage of the top five invasive species (*Casuarina equisetifolia* L., *Eichhornia crassipes* (Mart.) Solms, *Hydrilla verticillata* (L.f.) Royle, *Melaleuca quinquenervia* (Cav.) S.T.Blake, *Schinus terebinthifolius* Raddi) in Florida by 2014. Several contributing factors help explain the rapid spread of *L. microphyllum*, establishment and dominance in its introduced range. For example, *L. microphyllum* is able to produce copious amounts of viable spores year round that can travel over vast distances because of wind dispersal (Lott *et al.*, 2003; Volin *et al.*, 2004). Another important reason why *L. microphyllum* spreads quickly across South Florida's landscape is the fern's ability to reproduce by all three mating systems possible in homosporous ferns: intra- and inter-gametophytic selfing and outcrossing (Lott *et al.*, 2003). Moreover, female *L. microphyllum* gametophytes produce antheridiogen hormones (namely gibberellin) that prompt adjacent immature gametophytes to become male (Kurumatani *et al.*, 2001; Lott *et al.*, 2003).

Together with its prolific and plastic reproductive strategy, recent evidence shows that release from natural enemies may also contribute to the invasiveness of *L. microphyllum* (J.C. Volin & E.L. Kruger, unpubl. obs.). Finally, the fern seems to possess considerable phenotypic plasticity, allowing it to grow under a wide range of different environmental conditions. For instance, it maintains a similar growth rate in both low and high light levels (M.S. Lott & J.C. Volin, unpubl. obs.). While it grows mainly in wetlands that are periodically inundated such as cypress swamps, tree islands and/or pine flatwoods (Pemberton & Ferriter, 1998), it has also been found in relatively dry Florida scrub habitat (Roberts & Cox, 2000), although the latter appears to be contingent on vegetative spread from adjacent mesic habitats. It does not seem probable that young gametophytes and sporophytes could successfully develop independently on xeric sites. In any case, the apparent ability of *L. microphyllum* to grow under a vast array of different hydrological conditions has important implications for the Florida Everglades, which is undergoing a 30-year system-wide hydrological restoration.

A primary objective of the present study was to investigate growth characteristics of *L. microphyllum* under flooded, field capacity and drought condition in an effort to help explain the broad niche amplitude of *L. microphyllum* in its introduced range. Based on field observations, we hypothesised that the fern would grow faster under flooded hydrological conditions than in drought, as it occurs more frequently in periodically inundated areas of South Florida's environment, such as tree islands and bald cypress (*Taxodium distichum* (L.) Rich) sloughs. In these areas, *L. microphyllum* often establishes on microsites that are characterised by mesic conditions, such as those found on raised hummocks and/or cypress knees (J.C. Volin & M.S. Lott, personal observation). Thus, from these observations, the most favourable hydrological treatment would be field capacity, followed by the flooded condition. We also hypothesised that the least favourable hydrological condition would be drought, because *L. microphyllum*, a plant native to wetland habitats, does not seem to establish as well in xeric environments.

A complementary objective in our study was to elucidate the intrinsic causes underlying growth responses to the three hydrological treatments. Specifically, we monitored treatment effects on patterns of biomass allocation as well as the morphology and photosynthesis of fern pinnae. Additionally, to further explore the physiological basis for treatment responses, we tested the effects of exogenous applications of gibberellic acid (GA) and paclobutrazol (gibberellin inhibitor) on *L. microphyllum* growth and its principal determinants in the three hydrological treatments.

Bioactive forms of GA have been shown to modulate leaf expansion, stem elongation and biomass allocation patterns (e.g. Nagel & Lambers, 2002; Biemelt *et al.*, 2004; Bultynck & Lambers, 2004), and, in concert with other phytohormones, they appear to play a key role in plant stress responses (Vaadia, 1976; Steffens *et al.*, 2006). Several studies, for example, have indicated that endogenous GA levels are sensitive to excesses or deficiencies in soil moisture (Rood *et al.*, 2000; Dat *et al.*, 2004; Steffens *et al.*, 2006). Moreover, exogenous GA application has been shown to increase growth under flooded (Rijnders *et al.*, 1997; Dat *et al.*, 2004) and drought (Rai *et al.*, 1978, Pandey *et al.*, 2004) conditions. Paclobutrazol, on the other hand, often further suppresses growth under water stress (e.g. Fernández *et al.*, 2006; Navarro *et al.*, 2007). We hypothesised that, particularly in flooded and drought conditions, GA application would stimulate growth rate, owing primarily to increases in biomass allocation to leaves and/or specific leaf area (SLA), and that paclobutrazol application would have the opposite effect.

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Materials and methods

Plant materials

Fertile *Lygodium microphyllum* fronds were collected in October 2005 from an infestation located at the 'Big Cypress Seminole Indian Reservation' in Hendry County, Florida, USA. The fronds were dried at room temperature inside paper bags and spores were then released. The spores were collected and kept inside sterile centrifuge tubes. The spores were disinfected with 1% bleach and transferred to Petri dishes that contained Parker-Thomson Medium in April 2006. The plates were placed in an incubator set at 25–27°C under cool-white light illumination of approximately 100 μmol m^{-2} s^{-1} for 8 weeks and were watered with sterile deionised water every week. After 8 weeks, individual gametophytes were transferred to fresh Petri dishes (June 2006). Using a sterile spatula, 6–8 gametophytes were placed on each plate.

Sporophytes started to develop after 5 weeks. In August 2006, when the roots and leaves of the sporelings were well developed, 150 plants were transplanted to small pots previously filled with sterile sand. The 150 plants were placed in a growth room under white fluorescent illumination for approximately 6 weeks. The plants were kept very moist and humid, by using humidomes on top of each tray and watering them with half-strength Hoagland's nutrient solution as needed.

Experimental design

In October 2006, the plants were placed in a greenhouse at Florida Atlantic University, (Davie, FL, USA) where relative humidity was 75 ± 10% and air temperature averaged 25.0 ± 2°C. After 1 week of acclimation, 120 sporelings were transplanted to 2.5 L pots filled with soil collected from the rhizosphere of a *L. microphyllum*-infested site on the Big Cypress Seminole Indian Reservation. The soil's mean sediment class was determined to be a medium sand (Stewart 2002). Three hydrological and three growth regulator treatments were implemented using a 3 × 3 factorial experimental design. The three hydrological treatments were: 'flood,' where the water level in the pots was kept permanently 2 cm above soil level, 'field capacity,' where soil was kept moist by watering the plants as needed; and 'drought,' where plants were supplied with 150 mL of water or nutrient solution when their pre-dawn pinnae water potential (Ψ) reached approximately −1.0 MPa. We chose this Ψ threshold, based on results of a preliminary study, in order to expose plants to ecologically relevant levels of water stress and, at the same time, avoid permanent wilting.

In order to monitor the water status of the plants during the study, pre-dawn pinna Ψ was measured, with a Scholander pressure chamber (PMS, Corvallis, Oregon, USA), on 20 plants that were grown under the same conditions as the experimental plants. Ten grew under drought conditions, and five each under field capacity and flood. During the first week of the study, two to three different plants under drought conditions were measured every day. As the study progressed, at least two different drought plants were measured every 2–3 days. Whenever the plants under the drought treatment reached the desired minimum pre-dawn Ψ, plants under flood and field capacity were also measured (approximately once a week).

The three growth regulator treatments consisted of 1 μM GA_3 (one of the most widely used and biologically active gibberellins), 10 μM paclobutrazol, a GA biosynthesis inhibitor, and water (control). These growth regulator concentrations were similar to those used by Bultynck & Lambers, (2004) for two *Aegilops* species. In a preliminary test on non-experimental plants (maintained at field capacity), individuals sprayed with these concentrations three times weekly for 40 days exhibited no visually discernible responses to either chemical. The GA_3 (Acros Organics, min purity 99%) and paclobutrazol (ChemService, min purity 98.6%) solutions were prepared as in Khan *et al.* (2006).

Each growth regulator treatment was applied with a foliar sprayer to all above-ground parts of 27 plants (nine per hydrological treatment). Five millilitres of GA_3, paclobutrazol or water per plant (2.5 mL per spray × 2 applications) were applied 3 days a week for the duration of the study. All plants received the same amount of nutrient solution to allow for optimal growth. Namely, every other time that pre-dawn Ψ of the drought plants reached −1.0 MPa, plants were watered with 150 mL of half-strength Hoagland's solution (approximately every 2 weeks).

Measures of growth and its principal determinants

Two harvests were conducted during this study: one at the beginning of treatment (1 November 2006), and another after 62 days of treatment. Just prior to the initial harvest, total rachis length (sum of the length of all rachises) was measured on all plants in order to group individuals into one of six size categories. Equal numbers of plants from each category were then randomly assigned to one of the nine treatment combinations (3 hydrological × 3 growth regulator treatments, $n = 9$ per treatment) and to an initial harvest group. For the initial harvest, 15 plants were separated into roots, rhizomes, rachises and pinnae. Soil was washed

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from roots and all plant components were dried to a constant mass at 70°C.

The allometric relationship between total plant mass and total rachis length from the initial harvest ($y = 0.007x - 0.0191$, $r^2 = 0.89$, $P < 0.001$) was used to estimate the initial plant mass of all experimental plants and to subsequently calculate their relative growth rate (RGR). RGR (mg g^{-1} d^{-1}) was calculated for individual plants during the 62 day interval, where RGR = [ln (final dry mass) − ln (initial dry mass)]/ days.

Just before the final harvest, we measured gas exchange on one or two fully expanded pinnae, from three to six plants per treatment, using a Li-Cor 6400 portable photosynthesis system (Li-Cor Biosciences, Lincoln, NE, USA). Measurements were conducted from 0900–1100 h. The $C0_2$ concentration in the reference chamber was 400 μmol mol^{-1}, cuvette temperature was 26°C, and photosynthetic photon flux (provided by a red-blue LED array) was 600 μmol m^{-2} s^{-1}, which matched the maximum photon flux density in the greenhouse. At final harvest, plants were again separated into pinnae, rachises, rhizomes and roots. After all plant components were dried to a constant mass (at 70°C), they were weighed and pinna mass ratio (PMR, akin to leaf mass ratio), rachis mass ratio (RaMR), rhizome mass ratio (RhMR) and root mass ratio (RMR) were calculated as in Volin *et al.* (2002). SLA was also calculated after measuring the plant's pinnae area using a Li-Cor LI-3100 (Li-Cor Biosciences) leaf area meter.

Statistical analyses

A linear mixed-effect analysis of variance was used to assess the significance of differences in plant growth characteristics among treatments. Treatment main effects and their interactions were analysed using PROC MIXED in SAS (SAS Institute, Cary, NC, USA), based on a randomised complete block design. Unless stated otherwise, effects were considered to be significant when $P \leq 0.05$. The effect of block was not significant in any ANOVA. Regression analysis (employing PROC GLM in SAS) was used to examine possible influences of plant mass on RGR and its morphological, allocational and physiological determinants (Volin *et al.*, 2002). As is often the case (e.g. Mcconnaughay and Coleman, 1999; Volin *et al.*, 2002; Kruger & Volin, 2006), regression analysis indicated that RGR was negatively correlated ($P < 0.001$) with the natural log. (ln) of initial plant mass. Moreover, SLA, RaMR, RhMR and RMR at final harvest were all significantly related ($P < 0.01$) to final plant mass or its natural logarithm. Therefore, treatment effects on all of these parameters were assessed after each was normalised for variation in plant mass using analysis of covariance. Regression analysis was also used to assess relationships between RGR and its principal determinants.

Results

Treatment effects on plant water status

By the second week of treatment, a consistent temporal pattern emerged in the pinna water potential (Ψ) of plants under drought conditions; it typically reached an average of −1.0 MPa at pre-dawn 7 days after last watering (Fig. 1). Plants under flooded conditions and field capacity had very similar pre-dawn Ψ during the first 4 weeks, ranging from −0.25 to −0.5 MPa. However, after 35 days of treatment, and until the end of the study, plants under flooded conditions consistently had a lower Ψ than field capacity plants (Fig. 1).

Growth and physiological responses to treatment

We found no significant main effect or interaction attributable to GA_3 or paclobutrazol application for any plant variable measured in this study. Across growth regulator treatments, however, RGR was significantly lower in flooded plants compared with those in field capacity and drought treatments ($P < 0.001$, Fig. 2), while plants subjected to drought grew as rapidly as well-watered plants. RGR for flooded plants averaged 17.9 ± 3.5 mg g^{-1} d^{-1}. By comparison, plants growing under field capacity and drought conditions averaged 44.4 ± 2.6 and 44.2 ± 2.7 mg g^{-1} d^{-1}, respectively. Consequently, the dry mass of flooded plants at final harvest was roughly 75% less than that in the other treatments (data not shown).

Flooded plants also had significantly lower SLA than either field capacity ($P = 0.001$) or drought ($P < 0.001$) plants (Fig. 3). Plants under drought treat-

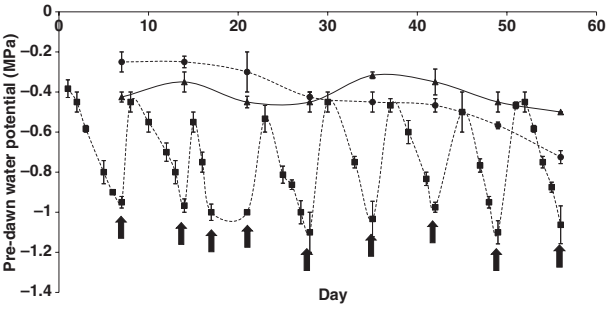

Fig. 1 Temporal dynamics in mean pre-dawn water potential (in MPa) for *Lygodium microphyllum* plants under flood (●), field capacity (▲) and drought (■) treatments. Arrows indicate watering events. Note that water potential was not assessed between the third and fourth watering.

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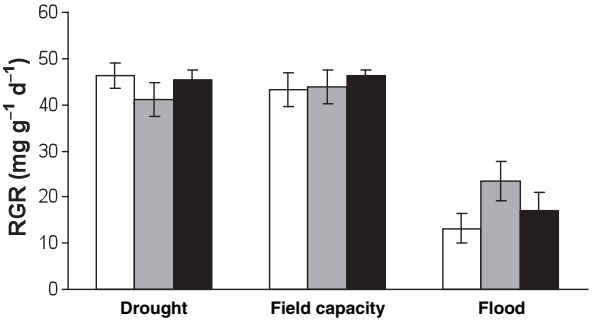

Fig. 2 Means (±SE) for relative growth rate (RGR) of *Lygodium microphyllum* plants under three hydrological (drought, field capacity and flood) and three growth regulator (control (□), gibberellic acid (▩) and paclobutrazol (■)) treatments.

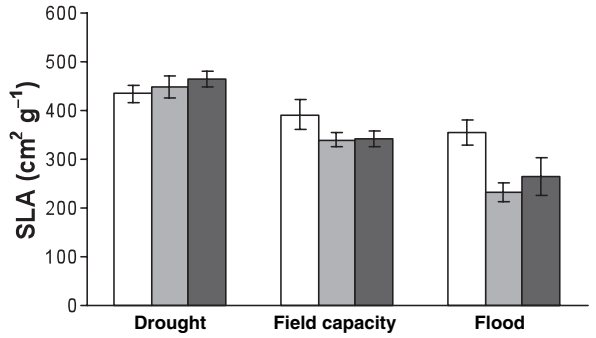

Fig. 3 Means (±SE) for specific leaf area (SLA) of *Lygodium microphyllum* plants under three hydrological (drought, field capacity and flood) and three growth regulator (control (□), gibberellic acid (▩) and paclobutrazol (■)) treatments.

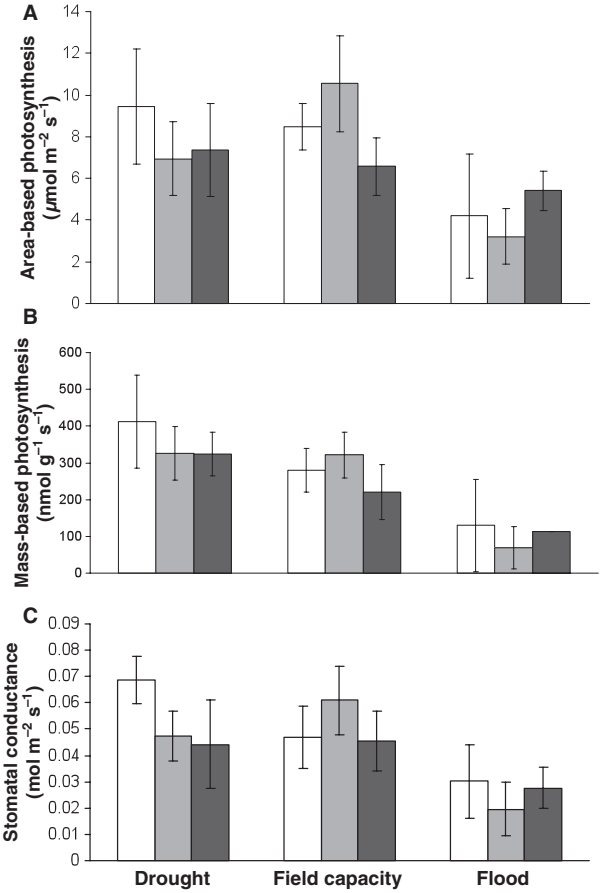

Fig. 4 Means (±SE) for area-based photosynthesis (A), mass-based photosynthesis (B) and stomatal conductance (C) of *Lygodium microphyllum* plants under three hydrological (drought, field capacity and flood) and three growth regulator (control (□), gibberellic acid (▩) and paclobutrazol (■)) treatments.

ment had a significantly higher SLA than field capacity plants ($P < 0.001$, Fig. 3). Treatment differences in area-based rates of pinna photosynthesis resembled those observed in RGR. Pinna photosynthetic rates for flooded plants were significantly lower than plants under field capacity ($P = 0.04$, Fig. 4A) and drought treatments ($P = 0.06$). Pinna photosynthesis for flooded plants averaged 4.5 ± 1.8 μmol m^{-2} s^{-1}, while field capacity and drought plants had very similar average photosynthetic rates (8.8 ± 1.7 and 8.4 ± 2.2 μmol m^{-2} s^{-1}, respectively). Similar treatment effects on stomatal conductance were also observed (Fig. 4C). As a consequence of parallel treatment effects on SLA and area-based pinna photosynthesis, mass-based rates of pinna photosynthesis in flooded plants were 64–72% lower than those of plants in field capacity and drought treatments ($P = 0.04$ and $P = 0.003$, Fig. 4B) Among the plant variables we measured, biomass allocation patterns responded the least to treatments. PMR did not respond significantly to treatment, and averaged 0.48 across all plants at final harvest (data not shown). The only biomass allocation variables that differed significantly among treatments were RaMR and RhMR. Relative to the respective mean for field capacity plants (0.11 for RhMR, and 0.22 for RaMR), RhMR was 28% lower in drought plants ($P = 0.01$), and RaMR was 14% lower in flooded plants ($P = 0.02$). Notably, at final harvest we also observed that a significantly greater percentage of plants were reproductive in the flood treatment than in either the drought or field capacity treatments (chi-square = 20.71; $P < 0.001$). For instance, 63% of flooded plants formed the initial stages of reproductive pinnae compared with only 11 and 4% of drought and field capacity plants, respectively.

Discussion

Growth responses to hydrology

Lygodium microphyllum is often found in forested wetlands in both its native and introduced range and our study results show that it is able to survive and

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become reproductive in a flooded environment, although it grows more slowly than in drier conditions. The low RGR of flooded *L. microphyllum* corresponded with low mass-based photosynthetic rates, which resulted from decreases in both SLA and area-based photosynthesis. In previous work, Dias-Filho and Reis De Carvalho (2000) found that *Brachiaria brizantha* (A.Rich.) Stapf also had a lower SLA when grown in flooded conditions. The causes for this response are unclear and our effort to explore potential gibberellin involvement (Biemelt *et al.*, 2004), using exogenous GA_3 and paclobutrazol application, yielded little additional insight. Alternatively, variation in SLA can be mediated by changes in leaf carbohydrates such as soluble sugar and/or starch accumulation (Lambers & Poorter, 1992; Dias-Filho and Reis De Carvalho, 2000) which is known to occur in flooded plants (Albrecht *et al.*, 1997; Dias-Filho and Reis De Carvalho, 2000). SLA may also have decreased because leaf cell expansion was inhibited owing to the onset of 'physiological drought' in flooded plants (Grubb, 1986).

Flooding of soil generally is followed by a decrease in the rate of photosynthesis in many angiosperm and gymnosperm species (Kozlowski, 1984; 1997). Some of the reduction in the photosynthesis of flooded plants is typically attributable to stomatal closure, resulting in decreased CO_2 supply to the mesophyll (Pezeshki *et al.*, 1996; Kozlowski, 1997). About 5 weeks into our study we observed a reduction in leaf water potential of flooded plants, which continued to the end of the study. The reduction in leaf water potential may have been a result of decreased hydraulic conductance in hypoxic or anoxic roots (Drew, 1997). In turn, low leaf water potentials possibly led to declines in stomatal conductance and, consequently, photosynthesis (observed after 60 days of treatment). In many species, however, flood-induced stomatal closure is not associated with a reduction in leaf turgor or leaf water potential (Kozlowski, 1997).

The absence of marked flooding effects on biomass allocation to pinnae is consistent with research on flooding responses of several different species (Miller & Zedler, 2003; Mahelka, 2006). The lack of fern response to GA_3 or paclobutrazol application contradicted our hypotheses, as well as previous findings indicating positive effects of GA_3 on RGR, LMR and SLA (Rijnders *et al.*, 1997; Bultynck & Lambers, 2004). We can not explain the absence of a hormonal influence, but studies have indicated that, in response to exogenous GA_3 application, plants can deactivate their endogenous bioactive GA production through a down-regulation of biosynthetic genes or elevation in degradative genes (Brock & Kaufman, 1988; Hedden & Phillips, 2000).

The large flooding-induced increase in sporangia production was one of the most interesting outcomes of our study. The causes of this response are unknown, but they likely involve changes in plant hormone levels. For example, ethylene synthesis commonly increases in flooded conditions and it can trigger several important flooding responses, such as the formation of aerenchyma and adventitious roots (e.g. Kozlowski, 1997; Baskin *et al.*, 2003; Dat *et al.*, 2004). Baskin *et al.* (2003) found that reproductive mechanisms in *Schoenoplectus hallii* (Gray) S.G. Sm. were activated during flooding conditions, because of an increase of ethylene production. Although this is not a ubiquitous phenomenon (Zeng *et al.*, 2006), it may explain the significantly higher reproductive output in flooded *L. microphyllum* plants. Moreover, this response could be adaptive, given that ample external moisture is needed in the spore reproductive cycle of this wetland-adapted climbing fern.

We anticipated that fern growth and physiology would be inhibited by drought, but apparently our water stress treatment was not severe enough to induce a pronounced response in *L. microphyllum*. The level of water stress we imposed, namely a periodic decrease in pre-dawn Ψ to -1 MPa, has been shown in a wide range of species (including other ferns) to induce marked responses, including stomatal closure and inhibited photosynthesis, altered biomass allocation, reduced stem elongation and leaf expansion, and decreased growth (Prange *et al.*, 1983; Schulze, 1986; Sharp & Davies, 1989; Hunt *et al.*, 2002). In light of this, the apparent tolerance of *L. microphyllum* to soil moisture stress deserves further scrutiny.

The results of our study highlight the hydrological plasticity of *L. microphyllum*. Even though *L. microphyllum* grew less vigorously under flooded conditions, it survived and became reproductive as well. Moreover, we observed no difference in growth between plants maintained at a constant water supply (field capacity) and those subjected to drier conditions (drought treatment). The ability of *L. microphyllum* to grow and become reproductive under different hydrological conditions has major implications for the Florida Everglades, a vast wetland, which is currently undergoing the largest hydrological restoration project ever attempted.

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