Flooding induces a suite of adaptive plastic responses in the grass Paspalum dilatatum

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Summary

- We studied individual responses to flooding in the perennial grass Paspalum dilatatum, a widespread species in the Flooding Pampa of Argentina, using plants established in species-diverse grassland microcosms.
- Flooding effects were evaluated on root and leaf sheath anatomy and shoot morphological traits. Leaf water status and CO2 exchange rates were monitored in flooded and unflooded plants under changing, natural and controlled atmospheric conditions.
- Root porosity and leaf sheath aerenchyma increased with flooding. Leaf extension rates and tiller height were also higher in flooded plants, which resulted in a large fraction of the shoot architecture emerging above the water surface. Flooding enhanced stomatal conductance, leaf water potential and net photosynthesis, especially under conditions leading to high air-vapour pressure deficits. Therefore, flooded plants experienced fewer water deficits during periods of high atmospheric evaporative demand.
- P. dilatatum showed tight regulation of water and carbon relations under severe soil-oxygen deficiency, even in the presence of natural competitors. The suite of adaptive responses documented here might help to explain the observed increase in abundance of this species during extensive floods.

Key words: aerenchyma, flooding tolerance, leaf growth, Pampa grasslands, Paspalum dilatatum, photosynthesis, tiller architecture, water relations.

Introduction

The potential for a plant species to persist within a multi-species community depends to a large extent on its ability to cope with prevailing abiotic constraints in the presence of neighbours (Weiher & Keddy, 1995; Bazzaz, 1996). Flooding acts as a powerful constraint on plant productivity and species composition in many natural habitats (Pennings & Callaway, 1992; Weiher & Keddy, 1995; Trebino et al., 1996; Gough & Grace, 1998). Whereas severe flooding typically causes a reduction in the abundance of flood-sensitive plant species, it can also promote biomass growth in flood-tolerant species (Insausti et al., 1999). In general, endurance of prolonged soil waterlogging may allow resistant plants to exploit resources that otherwise would be shared with nontolerant competitors (Crawford et al., 1989). Thus, in order to predict plant species dynamics in intermittently flooded habitats, a primary understanding of individual-based adaptations to tolerate or avoid waterlogging stress is needed (Osmond et al., 1987; Crawford et al., 1989; Blom et al., 1990).

Plants respond to flooding through changes at molecular, cell, tissue, organ and individual levels of organization. In flood-intolerant plant species, the lack of soil oxygen triggers a chain process that often results in severe physiological injury, as plant cells require oxygen for their normal metabolism (Jackson & Drew, 1984). In flood-tolerant plants, resistance to soil-oxygen deficiency can be achieved through various mechanisms, including anatomical, morphological, physiological and life-history adaptations (Blom et al., 1990; Pezeshki, 1994; Blom & Voosenek, 1996). Most flood-tolerant species
are capable of developing root aerenchyma in order to avoid tissue anoxia under waterlogging conditions (Justin & Armstrong, 1987; Blom et al., 1990). The elongation of stems and leaves is another plastic response commonly observed in flood-tolerant plants (Laan & Blom, 1990; Blom & Voesenek, 1996). Shoot extension and aerenchyma formation are both important for restoring the plant's contact with the atmosphere, and hence allowing internal oxygen transport to submersed organs during flooding periods (Blom & Voesenek, 1996).

In addition to these anatomical and morphological changes, flooding often disrupts plant water relations and gas exchange processes. Flood-intolerant species often show leaf dehydration in waterlogged soils, because oxygen deficiency reduces the cell-membrane permeability of the roots (Pezeshki, 1994; Tyerman et al., 1999). Many plant species also experience rapid declines in stomatal conductance when flooded (Kozlowski & Pallardy, 1984; Else et al., 1995). Since stomata closure causes diffusional limitation of carbon uptake, intolerant plants may have their photosynthetic capacity drastically reduced during extended floods (Kozlowski & Pallardy, 1984). Furthermore, flood-sensitive species can exhibit nonstomatal inhibition of photosynthesis, a process thought to be associated with alterations in plant hormone concentrations induced by tissue anoxia (Pezeshki, 1994). By contrast, flood-tolerant species may show little change, or even an increase, in carbon uptake rates during waterlogging periods (Naidoo & Naidoo, 1992). For example, the grass Sporobolus virginicus shows lower photosynthetic rates in well-drained soils than in flooded ones, as a result of increased levels of water stress (Naidoo & Naidoo, 1992). A tight regulation of the plant water status is thus required to maintain photosynthesis, nutrient uptake and growth in flooded environments (Kozlowski & Pallardy, 1984). Ultimately, flooding tolerance will reflect a suite of structural and physiological adaptations enabling the plant to remain functional under soil-oxygen deprivation (Jackson & Drew, 1984; Kozlowski & Pallardy, 1984; Blom et al., 1990; Blom & Voesenek, 1996).

In this paper, we investigate the effects of flooding on anatomical, morphological and physiological traits of the perennial grass Paspalum dilatatum, a common warm-season species in periodically flooded grasslands of the Argentine Pampas. P. dilatatum exhibits high resistance to waterlogging when grown in isolation (Rubio et al., 1995; Loreti & Oesterheld, 1996) and the capacity to increase in abundance within flooded plant communities (Insauti et al., 1999). However, little is known about the integration of morphological and physiological traits allowing this native grass to thrive under severe flooding in the presence of neighbours. Moreover, although previous work on P. dilatatum revealed patterns of biomass allocation and nutrient uptake indicative of drought tolerance (Rubio et al., 1995; Loreti & Oesterheld, 1996; Rubio & Lavado, 1999), there has been no attempt to assess how plants may adjust water and carbon relations to changing atmospheric conditions during extended floods. Our aim here was to evaluate individual responses to flooding compatible with the behaviour of P. dilatatum in natural plant communities. We hypothesized that a combination of anatomical, morphological and physiological responses minimizes the stress by flooding in this species. Specifically, we predicted that P. dilatatum would make better use of available water in flooded than in drained soils kept at field capacity. Thus, flooded plants would not develop substantial water deficits under conditions of high atmospheric evaporative demand.

Materials and Methods

Plant material and experimental design

Paspalum dilatatum Poir., is a conspicuous component of temperate humid grasslands of the Flooding Pampa in eastern Argentina. This native species is widely distributed across topographical gradients from upland communities on well-drained sandy soils, to lowland areas where various plant associations occur on annually flooded, fine-textured soils (Burkart et al., 1990). P. dilatatum is a highly productive C₄ grass with an extended growing season ranging from late spring, through summer to early autumn (Sala et al., 1981). We conducted an outdoor microcosm experiment using plants of P. dilatatum naturally established in soil monoliths extracted from a lowland grassland site (near Pila, Buenos Aires Province, Argentina). The use of microcosms helped overcome most problems concerned with manipulating soil waterlogging in the field, while it also allowed us to monitor individual plant responses in the presence of natural neighbours (Grimoldi et al., 1999).

Twenty plants of P. dilatatum of similar size and prostrate architecture were obtained during spring from a lowland grassland site grazed year-round by cattle. Each target plant was located at the centre of a 30 × 30 × 40 cm soil monolith supporting intact vegetation. The grassland was unflooded at the time of monolith extraction. Because of the restricted growth form of P. dilatatum, each plant was thought to represent a different clone within the same local population. Monoliths were transported to an experimental garden, where they were placed in plastic containers to manipulate artificial flooding. After a one-month acclimation period, monoliths were randomly assigned to two treatments: control – monoliths watered daily to field capacity and allowed to drain freely through holes drilled in the container; flooding – monoliths inundated with tap water and kept waterlogged to 6-cm height above soil surface (intact container) until the end of the experiment. Treatments ran for 45 d from late spring to early summer, and were replicated 10 times.

Leaf anatomy and root porosity

Root anatomy and aerenchyma formation in P. dilatatum were described elsewhere (Rubio et al., 1995). Therefore, we...
focus here on changes in leaf anatomy as induced by flooding. Segments of leaf sheath from the portion located 1 cm below the ligule were taken from each P. dilatatum plant at the end of the experiment, and were preserved in a FAA solution for later microscopical analysis. Leaf sheath sections c. 20 µm thick were cut freehand, stained with 50% water-soluble safranine and mounted in gelatine-glycerine. Similar leaf sheath segments were embedded in paraffin; longitudinal sections from the keel portion were cut with a rotatory microtome and stained with safranine-fast green. Five sections of leaf sheath were randomly selected from each plant for observation. Percentage aerenchymatous space (i.e. the ratio between the area occupied by aerenchyma and the total cross-sectional area) in the leaf sheath was measured using an optical microscope (Zeiss Axioplan, Zeiss, Oberkochen, Germany) connected to an image analyser (ImageneXtion Px, Imagereation Corp., Beaverton, OR, USA). In addition, the mean length of parenchymatous cells present along longitudinal sections of leaf sheath was measured under the optical microscope. The number of parenchymatous cells was evaluated for the same row used to measure cell length in leaf sheath sections of flooded and unflooded plants. The focal row of cells occurred between vascular bundles of identical size, and at the same depth in the sheath parenchyma, for the plants of both treatments. Microphotographs of this material were taken through the Zeiss Axioplan microscope. Measurements were performed on five randomly selected plants from each treatment, at the beginning of the experiment and after 45 d of flooding. Gas-filled root porosity was quantified for fresh samples of young roots taken from five plants per treatment using the pycnometer method (Sojka, 1988).

Shoot morphology

The leaf extension rate was recorded for all control and flooded plants over a one month period. Measurements of leaf length were taken to the nearest 0.1 cm on the youngest visible leaf (3rd or 4th, according to day of experiment) of three tillers per plant; each leaf was followed until the ligule was exposed. In addition, we measured the mean leaf blade and sheath length, and the mean tiller insertion angle and height (relative to the soil surface) of all P. dilatatum plants at the beginning of the experiment, after 10 days and at the end of the study. These measurements were performed on the third leaf (with ligule exposed) of 10 tillers per plant.

Stomatal conductance and leaf water potential

Stomatal conductance (g\(_s\)) was measured using a Li-1600 M steady state porometer (Li-Cor Inc., Lincoln, NE, USA). The two youngest fully expanded leaves of each plant were selected for measurement. Leaf water potential (Ψ\(_l\)) was recorded on the same leaves using a PI-6 Scholander-type pressure chamber (Bio-Control, Buenos Aires, Argentina); Ψ\(_l\) was measured immediately after completing the g\(_s\) measurements. Both Ψ\(_l\) and g\(_s\) were recorded approximately every second day, simultaneously with measures of leaf elongation. Air temperature and rh were monitored (Temperature & RH Probe HUMICAP H, Vaisala, Finland) and used to calculate the air vapour pressure deficit (VPD\(_a\)) at the time of each set of g\(_s\) and Ψ\(_l\) measurements. The ambient photosynthetic photon flux density (PPFD, over 400–700 nm) was recorded on each leaf simultaneously with g\(_s\) measurements using a point quantum sensor (Li-Cor Inc., Lincoln, NE, USA).

Gas exchange measurements

After 45 days under natural atmospheric conditions, eight microcosms from each treatment were moved into a temperature-humidity controlled glasshouse. The original treatments were maintained to examine how flooding affected the capacity of P. dilatatum plants to regulate gas exchange rates under different, controlled levels of atmospheric evaporative demand. Leaf stomatal conductance, transpiration rate and net photosynthesis (P\(_n\)) were recorded in flooded and control plants at low, medium and high VPD\(_a\) conditions. We modified experimentally the air temperature and humidity within the glasshouse to create a controlled gradient of evaporative demand (range, 0.5–4 kPa), and then measured plant parameters at three time steps corresponding to increasing levels of VPD\(_a\). Air vapour pressures were calculated from the rh and temperature conditions established in the glasshouse. The experiment was conducted over three consecutive days; this schedule allowed the plants to equilibrate to each new VPD\(_a\) level before measurement. Photosynthesis was measured as net CO\(_2\) exchange rate using a Li-6250 portable system (Li-Cor Inc.). For each plant, P\(_n\) measurements were taken on a portion of the youngest fully expanded leaf placed in a 250-cm\(^3\) chamber, with additional lighting from a 1500-µmol m\(^{-2}\) s\(^{-1}\) (PPFD) light source. The same leaves were used to record the transpiration rate, g\(_s\), and leaf temperature of flooded and unflooded plants at each VPD\(_a\) condition.

Statistical analyses

Anatomical variables were analysed using one-way ANOVA (n = 5); percentage data were arcsine square-root transformed before analysis (Steel & Torrie, 1988). Differences in shoot morphological traits (leaves and tillers) between control and flooded plants were assessed by two-way ANOVA (n = 10), with flooding treatment and measurement date (10 vs 45 d) as main factors. Tiller insertion angle and height data were square-root transformed to meet ANOVA assumptions. Effects of flooding on daily leaf elongation rates and physiological parameters measured outdoors (n = 10) were evaluated through repeated-measures ANOVA. The Greenhouse-Geysen correction was used to adjust for possible violations of the sphericity assumption (Von Ende, 1993). The relationship between
physiological parameters and atmospheric conditions ($VPD_{air}$) during the course of the outdoor experiment was examined by simple regression analysis, using the absolute difference in mean daily values of $g_s$ and $Ψ_l$ between flooded and control plants as the response variable. For the glasshouse experiment, differences in physiological parameters of flooded and control plants ($n = 8$) at increasing $VPD_{air}$ levels were tested by repeated-measures ANOVA (Potvin & Lechowicz, 1990; Von Ende, 1993). In these analyses, the flooding treatment was the between-subject factor and the level of $VPD_{air}$ represented the within-subject factor (Potvin & Lechowicz, 1990). All results are presented as mean ± standard error (SE).

**Results**

**Anatomical responses**

Leaf sheaths of control plants had little constitutive aerenchyma (Fig. 1a). However, flooding increased the area occupied by aerenchyma (Fig. 1b). Leaf sheath aerenchyma significantly increased from 2.5 ± 0.4% in control plants, to 19.7 ± 2.7% in flooded plants ($P < 0.001$). This expansion of aerenchymatous space resulted from cellular lysis in the keel (Fig. 1c), and the increased number and size of lacunae present in other zones of the sheath (Fig. 1b). Parenchyma cells in the leaf sheath of flooded plants were longer (97.8 ± 4.7 µm) than those of unflooded plants (74.8 ± 3.5 µm; $P = 0.01$). Moreover, the number of cells forming the designated layer of parenchymatous tissue (Fig. 2) was also significantly ($P < 0.005$) higher in flooded than in control plants (919.3 ± 61.2 vs 418.8 ± 76.0 cells, respectively). Root porosity was relatively high (33.7 ± 2.9%) in all plants at the beginning of the experiment; however, flooding increased gas-filled root porosity from 32.0 ± 0.9% in control plants to 40.7 ± 2.4% in flooded ones ($P < 0.02$).

**Morphological responses**

Repeated-measures ANOVA revealed that flooding significantly ($P < 0.005$) increased leaf elongation rates. A treatment × time effect ($P = 0.01$) indicated that differences in leaf growth between control and flooded plants increased during the experiment (Fig. 3). Two-way ANOVA showed significant effects of flooding treatment ($P < 0.0001$) and date of measurement ($P < 0.0001$) on mean blade and sheath length per plant. Although the leaves of flooded plants were already longer than those of control plants after 10 d of treatment (Fig. 4), differences in blade and sheath length increased towards the end of the experiment (flooding × date; $P < 0.0001$). Flooding increased ($P < 0.0001$) the mean insertion angle and height of individual tillers (Fig. 5). There was no significant treatment × date effect for these variables ($P > 0.30$; date: $P < 0.005$), indicating that differences in tiller architecture mainly developed during the first 10 d of the experiment. Tiller growth orientation under prolonged flooding shifted from the originally horizontal, prostrate position, to a more vertical one. This resulted in flooded plants having a larger fraction of their tiller length (c. 70%) above the water level (Fig. 5b).

**Physiological responses**

Stomatal conductance and leaf water potential. Repeated-measures ANOVA revealed significant effects of flooding ($P < 0.0001$) on $g_s$ and $Ψ_l$ (Fig. 6a,b). Differences in water status of control and flooded plants markedly changed through time (treatment × time: $P < 0.0001$; time effect: $P < 0.0001$), reflecting natural fluctuations in the atmospheric evaporative demand under outdoor conditions (Fig. 6c). Flooding effects on $g_s$ and $Ψ_l$, as measured by the absolute difference in mean daily values between flooded and control plants, were strongly

![Fig. 1](https://www.newphytologist.com) Leaf sheath cross-sections from *Paspalum dilatatum* plants grown for 45 d in (a) soil watered to field capacity, and (b) soil flooded to 6-cm height (scale bar, 180 µm); (c) magnified cross-section of leaf sheath showing flood-induced cellular lysis (scale bar, 20 µm). L: lacunae.
correlated with natural VPD air levels \((r = 0.917 \text{ and } 0.935, \text{ both } P < 0.0001, n = 21, \text{ for } g_s \text{ and } y, \text{ respectively})\). On average, flooded plants maintained higher values of \(g_s\) and \(y\) than control plants, although this mainly reflected differences occurring during periods of high VPD air when control plants suffered substantial declines in both physiological parameters (Fig. 6).

**Gas exchange rates** Repeated-measures ANOVA showed highly significant effects of flooding \((P < 0.0001)\) and VPD air \((P < 0.0001)\) on physiological variables recorded in the glasshouse experiment (Fig. 7). Moreover, significant flooding–VPD air interactions \((all \ P < 0.0001)\) indicated that differences in gas exchange rates between flooded and control plants became greater with higher levels of water vapour atmospheric...
Plants growing in flooded microcosms showed higher gs, transpiration and Pn than those watered to field capacity, when exposed to high VPDair conditions (Fig. 7a–c). Flooded and control plants did not differ in any of these variables under low VPDair levels. These responses were accompanied by a significant increase in leaf temperature across the VPDair gradient (Fig. 7d). However, notice that at high levels of VPDair, mean leaf temperature for flooded plants remained 6°C below that recorded for unflooded controls (flooding × VPDair interaction: P < 0.0001).

**Discussion**

Two processes are critically associated with a plant species ability to tolerate flooding: internal oxygen transport to prevent anoxia in submerged plant organs, and maintenance...
of root function to avoid inhibition of water and nutrients uptake. In periodically flooded habitats, tolerant plant species perform these tasks through various adaptive responses, which allow them not only to survive waterlogging periods (Blom et al., 1990; Naidoo & Naidoo, 1992; Pezeshki, 1994), but also to take competitive advantage over flood-sensitive neighbours (Crawford et al., 1989; Weih & Keddy, 1995). The present study shows that P. dilatatum has well-developed mechanisms to avoid stress by severe flooding. Individual plant responses to flooding in this species involved changes in leaf anatomy and shoot architecture, and the ability to maintain basic physiological processes over a range of atmospheric conditions. This high degree of functional plasticity allows P. dilatatum to grow during flooding periods, even when surrounded by natural competitors. The development of aerenchyma is considered the most important trait for a plant to tolerate soil anaerobiosis during extended floods (Jackson & Drew, 1984; Blom & Voesenek, 1996). Flooded P. dilatatum plants contain substantial amounts of aerenchyma in the root cortex (Rubio et al., 1995) and in leaf tissues (Fig. 1), forming an internal system of interconnected channels. The increased porosity found in the roots of flooded plants suggests that root tissues were rapidly supplied with extra-air upon submergence. This is consistent with the large fractions of constitutive root aerenchyma found in P. dilatatum clones from various lowland grasslands (Rubio et al., 1995; Loreti & Oesterheld, 1996). Internal oxygen supply to the roots becomes critically important as oxygen concentrations decrease in the flooded soil (Laan et al., 1990). Aerenchymatous tissues provide the plant with a low-resistance, air diffusion pathway that may enhance the oxygen supply to the roots. The existence of a well-developed system of air-filled intercellular spaces may also decrease oxygen requirements by reducing the amount of respiring tissues (Armstrong, 1979; Hsiao & Huang, 1989). Flooding changed the shoot architecture of P. dilatatum, increasing the amount of leaf and tiller area deployed above the water surface (Figs 4, 5). Similar morphological changes have been reported for other herbaceous species growing in periodically flooded habitats (Bleecker et al., 1986; Laan & Blom, 1990; Van der Sman et al., 1991; Naidoo & Naidoo, 1992; Grinstein et al., 1999). Several studies suggest that shoot elongation in submerged plants may be controlled by phytohormones, and in particular by ethylene production, as in flood-tolerant Rumex species (Van der Sman et al., 1991; Banga et al., 1996). Experiments conducted on isolated P. dilatatum plants showed that flooding may increase shoot height without substantial changes in total plant biomass (Rubio et al., 1995). Our study revealed various anatomical and architectural changes that may account for the remarkable shift in plant morphology induced by flooding in this grass species. The leaf sheath of flooded plants had greater numbers of longer aerenchymatous cells, which may explain the enhanced leaf elongation observed under flooding (Figs 3, 4). Bleecker et al. (1986) showed that shoot submergence in deepwater rice induces rapid internode elongation, a response involving an increase in both the number and length of internodal cells. We also found that the tillers of flooded plants shifted their insertion angles adopting a more upright position (Fig. 5). Such a plastic response has usually been associated with changes in red : far-red ratios of incoming light in the presence of neighbours (Gibson et al., 1992), but has rarely been reported as an adaptation to flooding. The development of longer leaves and stems, coupled with the vertical orientation of tillers, restored contact with the atmosphere in flooded plants, and thus contributed to maintain a diffusion pathway for oxygen transport from air-exposed organs to submerged roots. The use of atmospheric oxygen to maintain aerobiosis in root tissues is essential for a plant’s strategy to survive extended flooding (Laan et al., 1990).

We proposed at the outset that flooding tolerance in P. dilatatum would be associated with its ability to avoid the stress imposed by soil-oxygen deficiency and to regulate its water status during flooding periods. In flood-intolerant species, persistent root anoxia causes severe limitation in the energy available to maintain normal water and mineral uptake rates (Jackson & Drew, 1984). Our study revealed various anatomical and architectural changes that may account for the remarkable shift in plant morphology induced by flooding in this grass species. The leaf sheath of flooded plants had greater numbers of longer aerenchymatous cells, which may explain the enhanced leaf elongation observed under flooding (Figs 3, 4). Bleecker et al. (1986) showed that shoot submergence in deepwater rice induces rapid internode elongation, a response involving an increase in both the number and length of internodal cells. We also found that the tillers of flooded plants shifted their insertion angles adopting a more upright position (Fig. 5). Such a plastic response has usually been associated with changes in red : far-red ratios of incoming light in the presence of neighbours (Gibson et al., 1992), but has rarely been reported as an adaptation to flooding. The development of longer leaves and stems, coupled with the vertical orientation of tillers, restored contact with the atmosphere in flooded plants, and thus contributed to maintain a diffusion pathway for oxygen transport from air-exposed organs to submerged roots. The use of atmospheric oxygen to maintain aerobiosis in root tissues is essential for a plant’s strategy to survive extended flooding (Laan et al., 1990).

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possible, however, that hormonal effects were involved in the expression of this growth response (Voesenek et al., 1992). Because photosynthesis was always measured under high PPFD levels, differences in $P_n$ between flooded and control plants may be accounted for by differences in stomatal conductance (Fig. 7). Increased leaf temperatures at higher VPD$_{air}$ would contribute to enhance $P_n$ rates in this C$_4$ grass, as long as the process is not limited by stomata closure. Low stomatal conductance constrained CO$_2$ uptake in water-stressed, control plants, especially when these were exposed to high VPD$_{air}$ conditions. Such a stomatal response could reflect either a hydraulic effect (threshold $P_t$ exceeded) or a direct influence from the leaf-air gradient in water vapour pressure associated with high leaf temperatures (Lange et al., 1971; Else et al., 1995).

Our results add to previous work suggesting that the plastic responses that allow $P$. dilatatum to grow above ground during prolonged floods may not entail a cost in terms of resource acquisition below ground (Rubio et al., 1995; Rubio & Lavado, 1999). Furthermore, we demonstrate here that, when growing in flooded soil, this grass species has a remarkable capacity for regulating leaf water and carbon relations under highly changing atmospheric conditions. It must be noted, however, that in order to provide a more realistic assessment of adaptive responses to flooding, and unlike previous studies using potted plants, we have focused on the behaviour of $P$. dilatatum plants that were surrounded by assemblages of natural competitors. Visual observations during the experiment suggested that total above-ground biomass, and indeed interspecific competition on target plants, could be greater in flooded microcosms (Insauti et al., 1999). Thus, while some of the observed changes in the shoot architecture of $P$. dilatatum may have partly reflected the influence of neighbouring vegetation (Gibson et al., 1992; Rubio et al., 1995), it seems unreasonable to attribute the enhanced physiological adjustment of flooded plants to a modification in the competitive environment.

To summarize, the evidence reported here indicates that a suite of responses occurring at anatomical, morphological and physiological levels enables $P$. dilatatum to withstand severe flooding in the presence of neighbours. This has implications for the population dynamics of this grass species in periodically flooded environments. The ability to survive and grow during waterlogging periods provides a competitive advantage over less tolerant species (Crawford et al., 1989; Weih & Keddy, 1995) and may thus account for the biomass increase of $P$. dilatatum observed in flooded plant communities (Insauti et al., 1999). Nevertheless, within a community context, positive flooding effects on vegetative growth and nutrient status of flood-tolerant species (Rubio & Lavado, 1999) may also involve the use of soil resources released by mortality of non-tolerant neighbours. Such community feedbacks on the abundance of flood-resistant species deserve further experimental investigation.

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