Effects of Flooding and Drought on the Anatomy of *Paspalum dilatatum*

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Paspalum dilatatum occupies different topographic positions in the Flooding Pampa, Argentina. Populations from different positions are subjected to various regimes of flooding and drought, both of which may occur in the same growing season. We investigated the constitutive and plastic anatomical traits of *P. dilatatum* populations from habitats with contrasting regimes of flooding and drought. Both events affected root and sheath anatomy, and these effects were similar for clones from different topographic positions. Flooding increased the aerenchymatous tissue in the root cortex and the leaf sheaths and decreased the number of root hairs per unit of root length. Drought decreased the diameter of root metaxylem vessels, thus lowering the risk of embolisms and increasing water-flow resistance, and increased the number of root hairs, thereby increasing water uptake ability. In addition to these plastic responses, all clones showed constitutive characteristics that may confer an ability to withstand sudden events of flooding or drought: a high proportion of aerenchyma, which may maintain aeration before plastic responses take place; sclerenchyma, which may prevent root and leaf sheath collapse by soil compaction; and a conspicuous endodermis, which may protect stelar tissues from desiccation. Both constitutive and plastic anatomical characteristics are likely to contribute to the ability of this species to occupy widely different topographic positions and to resist temporal variations in water and oxygen availability.   © 2001 Annals of Botany Company

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INTRODUCTION

Plants respond to variations in the content of soil water and oxygen through morphological, anatomical and physiological adjustments that help them cope with such variations. This capability may have high survival value in plants from environments that experience frequent episodes of drought and flooding, such as some tropical savannas and temperate sub-humid grasslands (Sarmiento, 1984; Soriano, 1992).

There are both similarities and differences in the effects that flooding and drought have on plants. Due to the generation of hypoxia in the rhizosphere, flooding reduces water absorption and stomatal conductance causing flooding-sensitive plants to wilt in a similar way to drought (Jackson and Drew, 1984). However, flooded plants respond to this stress with developments that improve root aeration such as production of aerenchyma, development of adventitious roots, stem and leaf elongation, and epinasty which can reduce the likelihood of water stress (Jackson and Drew, 1984; Banga *et al.*, 1995). Many of these responses seem to be mediated by the accumulation of ethylene under hypoxia (Jackson and Drew, 1984; Blom and Voesenek, 1996; Drew, 1997). Thus, survival and reproduction of wetland plants under waterlogged conditions depends on their ability to transport oxygen from aerial to below-ground organs. This diffusion of atmospheric oxygen results in the maintenance

of root aerobic respiration, nutrient absorption (Jackson and Drew, 1984; Justin and Armstrong, 1987; Naidoo *et al.*, 1992; Baruch and Mérida, 1995; Jackson and Armstrong, 1999), and rhizosphere activity (Stoecker *et al.*, 1995). There are strong interspecific differences in the proportion of constitutive aerenchyma, suggesting aerenchyma has adaptive value: species from frequently flooded habitats show a much higher proportion of aerenchyma than species from habitats that rarely or never flood. In addition, species from frequently flooded habitats show increased ability to respond plastically to flooding with an increase in the proportion of aerenchyma (Justin and Armstrong, 1987). The aerenchyma can be schizogenous (formed by cell separation) or lysigenous (formed by partial breakdown of the cortex) (Jackson and Drew, 1984). The former is the outcome of highly regulated and species-specific patterns of cell separation and differential cell expansion that create spaces between cells. Lysigenous aerenchyma arises from spatially selective death of mature cells (Jackson and Armstrong, 1999).

Drought also affects a plant's metabolism and morphology, reducing growth and development. An important aspect of plant response to drought is that as soil water availability declines, hydraulic tension along the soil-plant-atmosphere continuum increases to a point at which continuity of xylem water columns is lost by cavitation and water transport is reduced or interrupted (Tyree and Sperry, 1989; Higgs and Wood, 1995; Atkinson and Taylor, 1996). The limit to xylem tension before cavitation takes place depends, in part, on conduit size (Atkinson and Taylor, 1996). Conduits with larger diameters are more

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prone to cavitation than those with smaller diameters (Zimmerman, 1983; Carlquist, 1988). Thus, a xylem with narrow vessels is physiologically better protected against cavitation (Rury and Dickinson, 1984). As in the case of aerenchyma and flooding, there are interspecific differences in vessel diameter that suggest its adaptive value: woody species from drier habitats have narrower vessels than species from more humid habitats (Carlquist, 1988, 1989). However, in contrast to the responses of aerenchyma to flooding, plastic responses in vessel diameter have not been studied in drought-stressed grasses.

The development of root hairs depends to a large extent on the degree of humidity in the vicinity of the root (Uphof and Hummel, 1962). Consequently, we expect that species living in habitats where flooding and drought alternate will be under a strong selective pressure to develop the ability to adjust their anatomy and physiology according to the stress under which they are growing.

Paspalum dilatatum Poir., a grass occupying all available positions on a topographic gradient in the Flooding Pampa (Argentina), provides an opportunity to investigate the anatomical responses to flooding and drought and intraspecific variation in these responses. Some populations of this species live in habitats that are never flooded, others live in habitats that are regularly flooded for several months, and yet others live in intermediate situations (Cabrera, 1970; Lemcoff *et al.*, 1978; Burkart *et al.*, 1990). The effect that flooding has on some root characteristics was investigated in this species from an intermediate site (Rubio *et al.*, 1995): roots had constitutive aerenchyma that increased with flooding. Loreti and Oesterheld (1996) showed that root porosity, assessed by a pycnometer, increased under flooding and decreased under drought in plants collected in the three types of habitats listed above. The objective of this study was to investigate further the anatomy and anatomical responses to flooding and drought on roots and leaf sheaths of clones of *P. dilatatum* from different positions along a topographic gradient in the Flooding Pampa grasslands.

MATERIALS AND METHODS

We performed a factorial experiment with clones of *Paspalum dilatatum* Poir. (Poaceae) which were taken from three different sites along a topographic gradient and subjected to three experimental water regimes: drought, field capacity, and flooding. The three sites, located in the centre of the Flooding Pampa of Argentina (36° S 58° W), are occupied by different plant communities (Burkart *et al.*, 1990): the upland site never floods, the intermediate site floods for certain periods almost every year, and the lowland site floods more frequently and for longer periods than the intermediate site. The three communities experience summer drought (Loreti, unpubl. res.). At each site we collected 20 ramets which, because of the tussock growth form of the species, are assumed to belong to genetically different clones. The clones were cultivated and propagated in a greenhouse for 7 months, a time considered long enough for acclimation (Loreti and Oesterheld, 1996). The experiment was a three × three factorial. Water was the

'treatment' factor and site of origin the 'classification' factor (Hulbert, 1984). Water was supplied at three levels: drought, field capacity (control), and flooding; and plants originated from one of three sites: upland, intermediate, and lowland site. Each combination of water × origin had 20 true replicates (clones) for the intermediate and lowland sites and 18 for the upland site. Not all clones are analysed in this paper.

Experimental plants were grown on washed sand in 16 cm tall × 11 cm diameter plastic pots without drainage holes. Pots in the flooded treatment permanently had water about 2 cm above their surface ($\theta = 34\%$ volumetric water content). Control pots were held at $\theta = 8\text{--}11\%$ which corresponds to field capacity in sandy soils (Hillel, 1971). Pots in the drought treatment were maintained at $\theta = 2\text{--}5\%$. All plants received 50 ml of Hoagland's solution number 2 weekly divided in five doses of 10 ml each.

Plants were harvested on day 50, the end of the experiment. Roots were washed carefully. Roots of uniform appearance (colour and texture) and diameter were chosen to minimize the possibility of comparing roots that originated at different times during the experiment. Root sections were cut 30 ± 3 mm from the root tip. Segments of leaf sheaths from the basal portion of the tiller, which was permanently waterlogged in the flooded plants, were also cut. These tissues were preserved in formalin - acetic acid - ethanol - water $(5:5:60:30)$ until processing for optical microscopy. Freehand sections about 20 μm thick from roots and leaf sheaths were stained with 50 % water-soluble safranin and mounted in gelatin-glycerine. For each clone, five to ten sections were selected at random for observation. The following measurements were performed using an optical microscope (Zeiss Axioplan, Zeiss, Oberkochen, Germany) connected to an image analyser (Imagenation Px, Imagenation Corporation, Beaverton, Oregon, USA): (1) percentage of aerenchyma in roots and leaf sheaths (ratio between the area occupied by aerenchyma and total cross sectional area); (2) diameter of inner (i. e. largest, cf. Fig. 1 D–E) metaxylem vessels (cell wall not included; Carlquist, 1988); and (3) the number of root hairs in the section's plane along one quarter of the section's perimeter. This figure was then transformed into number of hairs mm^{-1}. For each variable, the statistical significance of the differences among treatments and origins was determined by a two-way ANOVA and Tukey's test.

RESULTS

Root structure was affected by both drought and flooding. The structure of the leaf sheath was affected only by flooding. In contrast, the effect of site of origin and the interaction between the two factors were not significant ($P = 0\cdot10$ or greater, depending on response variable and treatment). Thus, data for different sites of origin were pooled for further analyses.

Roots

The roots of *P. dilatatum* showed large constitutive lacunae (aerenchyma). In the root cortex of control plants,
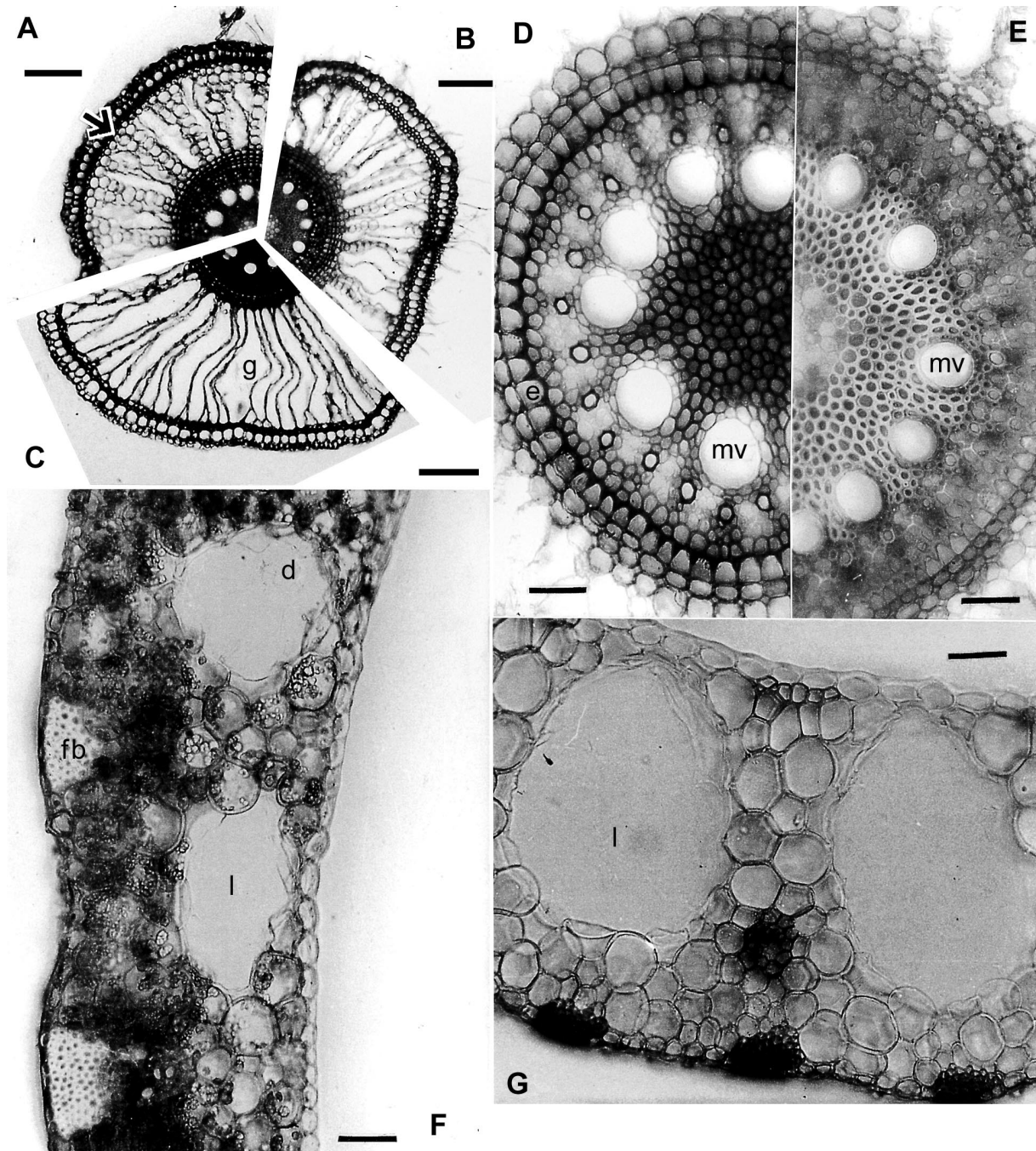
FIG. 1. Root anatomy of *Paspalum dilatatum* grown for 50 d in sand at field capacity (A, D), or subjected to drought (B, E) or flooding (C). Sections were taken at 30 $\pm$ 3 mm from the root tip. e, Endodermis; g, gas space; mv, metaxylem vessels. The arrow indicates the ring of elongated sclerenchymatous cells. Bar = 180 μm (A – C), 45 μm (D and E). F and G, Leaf sheath anatomy of *P. dilatatum* grown for 50 d in sand at field capacity (F) or flooded (G) on leaf sheath anatomy of *P. dilatatum*. Sections were taken at the basal portion of the tiller (F: abaxial side on the left; G: abaxial side at bottom). d, Diaphragms; fb, fibre bundles; l, lacunae. Bar = 45 μm.

there were radial files of cells leaving gas spaces between them, and some cells appeared deflated (Fig. 1A). In cross-section, there was a ring of elongated sclerenchymatous cells below the exodermis (Fig. 1A, arrow). Around the central cylinder, there was a conspicuous endodermis and three–four layers of parenchymatic cells outside it, whereas inside the central cylinder there was a large zone of sclerenchyma (Fig. 1D).

Flooding increased significantly (by 44 %) the proportion of aerenchyma in the root cortex ($F_{2,23} = 3\cdot7$; $P = 0\cdot04$); (Fig. 1C, Table 1). This additional aerenchyma apparently resulted from cell lysis and cell deflation. The amount of

TABLE 1. *Anatomical changes in* Paspalum dilatatum *following 50 d growth in sand at field capacity (control), or subjected to drought or flooding*

Parameter	Treatment		
	Drought	Control	Flooding
% Aerenchyma in roots (†)	$13 \cdot 3 \pm 1 \cdot 9^a$ (11)	$18 \cdot 5 \pm 1 \cdot 8^a$ (12)	$26 \cdot 7 \pm 3 \cdot 53^b$ (9)
% Aerenchyma in leaf sheaths (†)	$14 \cdot 3 \pm 0 \cdot 1^a$ (9)	$13 \cdot 1 \pm 0 \cdot 5^a$ (9)	$21 \cdot 1 \pm 1 \cdot 0^b$ (9)
Diameter of root vessels (μm) (*)	$33 \cdot 3 \pm 0 \cdot 5^a$ (12)	$42 \cdot 2 \pm 0 \cdot 3^b$ (12)	$40 \cdot 1 \pm 0 \cdot 4^b$ (10)
Root hairs (hairs mm^{-1}) (†)	$37 \cdot 4 \pm 2 \cdot 6^a$ (10)	$22 \cdot 5 \pm 1 \cdot 3^b$ (10)	$12 \cdot 9 \pm 3 \cdot 2^c$ (10)

Different superscripts in the same row indicate a significant difference $P < 0 \cdot 05$ (Tukey *t*-test).
Mean values $\pm$ s.e. Numbers in parentheses are number of clones. Values for each clone are averages of ten (*) or five measurements (†).

aerenchyma in droughted plants was slightly lower than in control plants, but this difference was not significant (Fig. 1B, Table 1).

The number of root hairs increased under drought and decreased under flooding ($F_{2,29} = 47 \cdot 05$; $P = 1 \cdot 6 \times 10^{-9}$; Table 1, Fig. 1B and C). Drought decreased the diameter of root metaxylem vessels by 22 % ($F_{2,27} = 4 \cdot 3$; $P = 0 \cdot 02$, Table 1, Fig. 1D and E). This represents a 38 % reduction in cross-sectional area.

Leaf sheaths

Large constitutive lacunae (aerenchyma) with diaphragms were found among the vascular bundles in the cross-section of leaf sheaths of *P. dilatatum*.

Flooding increased the area occupied by aerenchyma by 60 % ($F_{2,26} = 10 \cdot 8$; $P = 0 \cdot 0008$; Table 1, Fig. 1F and G) through an increase in the size of the lacunae. No significant differences were found between drought-stressed and control plants (Table 1).

DISCUSSION

Paspalum dilatatum responded to flooding by increasing root and leaf sheath aerenchyma and to drought by decreasing the diameter of metaxylem vessels. Moreover, the number of root hairs increased under drought and decreased under flooding.

Increased aerenchyma is a common adaptive response of plants to soil anoxia (Jackson and Drew, 1984; Justin and Armstrong, 1987; Jackson and Armstrong, 1999). In *Paspalum dilatatum*, aerenchyma produced under flooding was formed by cell lysis and cell deflation. The aerenchyma found in both sheaths and roots provides an interconnected system of air channels, enabling gases to diffuse or ventilate from above-ground to below-ground organs, and thus helping to maintain aerobic respiration and rhizosphere oxygenation (Blom and Voesenek, 1996; Jackson and Armstrong, 1999). This characteristic is essential for survival of plants that grow in flood-prone soils.

The proportion of aerenchyma often distinguishes flood-tolerant from flood-intolerant plants. In wetland plants, there is a large proportion of aerenchyma in above-ground and below-ground organs (Pezeshki, 1994). In contrast, most non-wetland species have root porosity below 7 % (Justin and Armstrong, 1987). The high proportion of constitutive aerenchyma in roots and sheaths of *P. dilatatum* is comparable to that observed in typical wetlands species.

While clones from different positions along the hydric gradient showed no differences in the proportion of aerenchyma, they exhibited a differential response to flooding in terms of growth (Loreti and Oesterheld, 1996): flooding reduced growth of clones from the upland site by 11 %, increased it by 10 % in clones from the lowland site, and did not affect growth in clones from the intermediate site. Thus, the differential growth response cannot be explained by anatomical changes, at least in the traits we investigated. However, the overall high tolerance of this species to flooding (-11 to $+10$ % range) can obviously be related to both the high level of constitutive aerenchyma and the ability to increase levels through cell lysis.

While aerenchyma formation can overcome the effects of hypoxia, it may also weaken the root structure. After flooding, when the soil becomes more compacted, the aerenchymatous structure may collapse under external pressure and the amount of functional root tissue may be reduced (Engelaar *et al.*, 1993). In addition, trampling by cattle increases soil density in the Flooding Pampa (Taboada and Lavado, 1993). The cortical sclerenchymatous cells of *Paspalum dilatatum* may help prevent the collapse of the cortex by soil compaction. In the leaf sheaths, this role would be played by the diaphragms and fibre bundles, which would strengthen the lacunal tissue (Sculthorpe, 1967).

We found that the diameter of root xylem vessels in *Paspalum dilatatum* decreased significantly under drought. To our knowledge, this is the first report of such a plastic response to drought in grasses. Vessel diameter seems to be closely and positively correlated with the volume of water conveyed and inversely correlated with the 'safety' of the conductive system (Carlquist, 1980; Salleo and Lo Gullo, 1986). Vessel embolism is more likely to occur in larger vessels as tension develops under water deficit, resulting in cavitation (Tyree and Sperry, 1989; Atkinson and Taylor, 1996). Narrower vessels maintain water columns under higher tension because they have a greater surface to volume

ratio, and a higher proportion of water molecules are bonded to the wall (Carlquist, 1989). Narrower vessels may also increase the resistance to water flow, which might be advantageous under drought. Formation of narrow vessels in late-wood often occurs in drought-tolerant dicotyledons (woody, short-lived perennials and annuals with secondary structure) (Carlquist, 1985; Arnold and Mauseth, 1999). The adaptive value of producing narrow vessels lies in an increased safety of water columns in narrower capillaries, which would be plastically achieved at least in *Paspalum dilatatum*. By reducing the risk of embolisms, the drought effect is retarded. The exodermis might be expected to have a protective function (as does the endodermis) during drought and to protect the roots from attack by soil pathogens (Peterson, 1992; Stasovski and Peterson, 1993). The presence of a conspicuous endodermis may play a role in preventing the collapse of the inner portion of the root and in protecting stelar tissues from desiccation, as has been found in roots exposed to drying soil (Sharp and Davies, 1985; Peterson, 1992; Allaway and Ashford, 1996).

We also found that the density of root hairs shows a plastic response. The development of root hairs depends to a large extent on the degree of humidity in the vicinity of the root; the number of root hairs per unit of length decreases with a high degree of humidity and increases with low humidity (Uphof and Hummel, 1962). Increased numbers of root hairs under drought may compensate for the lower water availability through the extension of the absorbing surface of the root, which would sustain the levels of water and nutrient uptake. The reduced number of root hairs under flooding probably relates to a lower restriction of water and nutrient movement to the root surface and the consequently smaller role played by the exploration of new microsites by roots.

In conclusion, the survival of *Paspalum dilatatum* in different topographic positions in the Flooding Pampa, with its inherent regime of flooding and drought, results from both constitutive anatomical characteristics and the ability to exhibit plastic responses to disturbance events.

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