CONSTITUTIVE AND PLASTIC ROOT TRAITS AND THEIR ROLE IN DIFFERENTIAL TOLERANCE TO SOIL FLOODING AMONG COEXISTING SPECIES OF A LOWLAND GRASSLAND

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Natural flooding is a major component of the disturbance regime in many grassland ecosystems. The objective of this study was to analyze the relationship among constitutive and plastic root traits and tolerance to flooding in coexisting perennial species of the flooding pampa grasslands (Argentina). A mesocosm experiment was designed for five native species (Paspalidium paludivagum, Paspalum dilatatum, Bothriochloa laguroides, Eryngium ebracteatum, and Eclipta bellidoide) and two exotic ones (Mentha pulegium and Plantago lanceolata). Across species, constitutive root porosity was positively correlated with the tolerance to soil flooding. Moreover, the generation of additional aerenchyma was larger in species with intermediate values of constitutive root porosity and lower in species with low or high constitutive root porosity. This differential increase in the root porosity of each species, combined with the values of constitutive root porosity, resulted in a stronger correlation between final root porosity and tolerance under flooding conditions. Native grasses increased the proportion of root aerenchyma, showing a small change in the number of lysed cells but a significant increase in the cortex proportion and diameter of roots. Exotic dicots generated lysigenous aerenchyma throughout their cortex; in contrast, native dicot species maintained the cell layers adjacent to the stele. A lag in the development of secondary growth during flooding was detected in both groups of dicots, a response that was particularly evident in the exotic species, contrasting with their prominent growth under nonflooded conditions. In general, our results indicate that constitutive and plastic root traits are very significant in terms of the effects of periodic flooding on the abundance of coexisting species of the flooding pampa grasslands.

Keywords: aerenchyma configuration, anaerobiosis, root porosity, flooding pampa grasslands, lysigenous aerenchyma, root diameter, secondary growth.

Introduction

Natural flooding is one of the major factors affecting structure and floristic composition in many lowland grasslands of the world. Plants inhabiting these grasslands have to deal with extreme changes in soil conditions during the year. In addition to inherent constitutive traits, it is known that specific plastic responses could increase the tolerance to environmental restrictions as a solution to temporary heterogeneous environments (Bradshaw 1963; Via et al. 1995). The importance of plastic responses to cope with changes in environmental conditions has been widely discussed, and the classic examples include responses to variation from disturbances, successional changes, or invasions of new areas (for review, see Bradshaw 1963; Via et al. 1995). Most flood responses are plastic and in herbaceous species frequently involve generation of additional aerenchyma tissue (Smirnoff and Crawford 1983; Justin and Armstrong 1987), formation of adventitious roots near the water level (Visser et al. 1996), and epinasty followed by later elongation of the aerial organs (Grimoldi et al. 1999; Cox et al. 2003). Epinasty and elongation responses are important for the recovery of contact with the aerial environment (Laan and Blom 1990; Van der Sman et al. 1991). Meanwhile, aerenchyma generation allows the continuous conduction of air from the nonsubmerged parts toward the roots, thereby contributing to increased survival under conditions of partial submergence (Laan et al. 1990).

Traits associated with flooding tolerance vary extensively among species, showing marked differences in their expression, amplitude, and time of responses. These differences have been examined mainly in comparative studies among individuals of different species (Justin and Armstrong 1987; Laan et al. 1989; Visser et al. 1996; and others) or populations (Vasellati et al. 2001) inhabiting areas with contrasting hydric regimes, but very few studies have focused on species that share the same habitat (Van der Sman et al. 1988, 1993). Generally, the proportion of root porosity in different species is closely related to the frequency of flooding in their natural habitat (Smirnoff and Crawford 1983; Justin and Armstrong 1987; Laan et al. 1989; Baruch and Mérida 1995; Visser et al. 1996; He et al. 1999). Moreover, in comparative...
studies with species of the genus *Rumex* inhabiting different areas of the river forelands in the Netherlands, the different capacity to elongate and increase the height of aerial organs in conditions of partial submergence was also positively related to the frequency of flooding events (Voesehek et al. 1989; Laan and Blom 1990). Accordingly, when comparing the responses of *Chenopodium rubrum*, *Rumex palustris* and *Rumex maritimus*, all three coexisting in low-elevation communities, the effects of flooding in each species depended on the flooding regime (i.e., intensity, duration, and frequency), which varied substantially from year to year (Van der Sman et al. 1988, 1993).

Because of the differential tolerance to flooding among species, great changes in the structure and floristic composition of the plant community can be expected (Crawford et al. 1989; Weiher and Keddy 1995; Insausti et al. 1999). A study in a lowland community of the flooding pampa grasslands demonstrated that natural flooding reverses, in a short period of time, changes in vegetation produced by cattle grazing (Insausti et al. 1999). In these grasslands, grazing of large herbivores provokes the increase in exotic dicots, such as *Leontodon taraxacoides*, *Plantago lanceolata*, or *Mentha pulegium* (Sala et al. 1986), which can represent up to 50% of the aboveground biomass in lowland communities (Chaneton et al. 1988). Natural flooding provokes marked decreases of these species, while most native species, generally grasses, are less affected or are favored by the occurrence of this disturbance (Insausti and Soriano 1987; Chaneton et al. 1988; Insausti et al. 1999). There is very little information about the constitutive and plastic anatomical traits regarding the effects of flooding on species of these grasslands. This aspect is particularly relevant when one considers the strong influences of prolonged flooding on plant community dynamics and that periodic flooding could be regarded as a natural subsidy to maintain the floristic composition of these grasslands (Insausti et al. 1999).

The objective of this article was to study the relationship among constitutive and plastic anatomical root traits and tolerance to flooding in coexisting species of the flooding pampa grasslands (Argentina). To this end, a mesocosm experiment was designed including seven perennial herbaceous species of these grasslands: five native species, *Paspalidium paludivagum*, *Paspalum dilatatum*, *Bothriochloa laguroides*, *Eryngium ebracteatum*, and *Eclipta bellidioides*, and two exotic species, *M. pulegium* and *P. lanceolata* (table 1). The selected species are representative of the region and known to have different levels of tolerance to soil flooding based on their performance in previous studies under natural flooding conditions (Insausti and Soriano 1987; Chaneton et al. 1988; Burkart et al. 1990; Insausti et al. 1999). More specifically, we addressed the following question: do the constitutive traits of a root system and its plasticity induced by soil flooding explain the level of tolerance of a plant species to soil flooding and thereby its abundance in the field?

### Material and Methods

#### Study Site and Plant Material

Natural grasslands of the Flooding Pampa cover a wide region dedicated mostly to cattle grazing. Climate is temperate subhumid. Mean annual rainfall is ca. 900 mm, evenly distributed through the year; however, variations between years are large. Mean monthly temperatures range from 6.8°C in August to 21.8°C in January. Plants used in this study were taken from a natural lowland grassland located in the Department of Pila, Province of Buenos Aires, Argentina (36°30'S, 58°30'W). Plants were collected from a stand of the plant community defined phytosociologically as the community of *Piptochaetium montevideonsis*, *Ambrosia tenuifolia*, *Eclipta bellidioides*, and *Mentha pulegium* (sensu Burkart et al. 1990). At this site, native grasses and sedges (graminoids) share community dominance with numerous perennial dicot species, many of which are exotic in the region. Such communities are found in flat areas, associated with soil fine texture and imperfect drainage (Lavado and Taboada 1988). Short floods (1–2 mo) of 5–7-cm depth occur at the beginning of almost every spring. Nonetheless, severe droughts may occur in early summer. The soil was a typical Natraquoll characterized by a nonsaline A$_1$ horizon with 2.6% organic carbon and low values of soil electrical conductivity (1.05 ± 0.04 dS m$^{-1}$) and by a natric B$_{2s}$ horizon at 0.2-cm depth with 53.3% clay content. At the same site, 2 mo of flooding decreased the soil redox potential from moderate reductive ranges (234 ± 8 mV) to highly reductive (−135 ± 6 mV) (Taboada and Lavado 1986). The reductive status of the soil during flooding corresponds to conditions that severely affected growth of most non-flood-tolerant species (Ponnamperuma 1984).

A controlled experiment was carried out with individuals of seven representative species of these grasslands: five native

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Origin</th>
<th>Flood tolerance in field studies</th>
<th>Vegetative growth habit</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Paspalidium paludivagum</em></td>
<td>Poaceae</td>
<td>Native</td>
<td>High</td>
<td>Stoloniferous grass</td>
</tr>
<tr>
<td><em>Paspalum dilatatum</em></td>
<td>Poaceae</td>
<td>Native</td>
<td>High</td>
<td>Bunch grass</td>
</tr>
<tr>
<td><em>Bothriochloa laguroides</em></td>
<td>Poaceae</td>
<td>Native</td>
<td>Low</td>
<td>Bunch grass</td>
</tr>
<tr>
<td><em>Eryngium ebracteatum</em></td>
<td>Apiaceae</td>
<td>Native</td>
<td>High</td>
<td>Rosette</td>
</tr>
<tr>
<td><em>Eclipta bellidioides</em></td>
<td>Asteraceae</td>
<td>Native</td>
<td>Medium</td>
<td>Creeping forb</td>
</tr>
<tr>
<td><em>Mentha pulegium</em></td>
<td>Lamiaceae</td>
<td>Exotic</td>
<td>Medium</td>
<td>Creeping forb</td>
</tr>
<tr>
<td><em>Plantago lanceolata</em></td>
<td>Plantaginaceae</td>
<td>Exotic</td>
<td>Low</td>
<td>Rosette</td>
</tr>
</tbody>
</table>

Note. All species are perennials. Flood tolerance in field studies is from previous reports at the community level by Insausti and Soriano (1987), Chaneton et al. (1988), Burkart et al. (1990), and Insausti et al. (1999).
species, *Paspalidium paludivagum* (Hitch. et Chase) Parodi, *Paspalum dilatatum* Poir., *Bothriochloa laguroides* (DC.) Pilger., *Eryngium ebracteatum* Lam., and *E. bellidioides* (Spreng.) Sch. Bip., and two exotic, *M. pulegium* L. and *Plantago lanceolata* L. (Table 1). All species are perennials and abundant in the studied plant community. *Paspalidium paludivagum* is characterized by the presence of long stolons and the formation of grassland lawns; *P. dilatatum* and *B. laguroides* are bunch-type grass. *Eryngium ebracteatum* and *P. lanceolatum* are creeping forbs with clonal growth capacity and propagation. Both exotic species originated in Europe, where *P. lanceolata* shows a wide distribution, while *M. pulegium* is restricted to humid locations subjected to periodical flooding (Hess et al. 1970).

**Experimental Design**

At the beginning of spring, uniformly sized individuals of each target species were extracted in rectangular soil blocks of 0.3 × 0.2 × 0.2-m depth, taking as the center the selected individual. Such blocks, considered “mesocosms,” were immediately placed in waterproof plastic containers and then transferred outdoors in the experimental garden of the Faculty of Agronomy at the University of Buenos Aires. The presence of a horizon B2t at 0.2-m depth in the soil profile with a minimum presence of roots assured the collection of most of the underground system of the selected individual. The use of mesocosms helped overcome the problems of flooding simulation in field conditions and of keeping the control blocks watered (Grimaldi et al. 1999; Insausti et al. 2001). After a 2-mo acclimation period, each replication was randomly assigned to one of the following treatments for 60 d: (1) control, watered daily to field capacity, or (2) artificial flooding, maintaining a constant 6-cm water layer above the ground surface. Each mesocosm constituted an experimental unit, and 10 replications per treatment and species were carried out. Soil volumetric hydric content of the control blocks was monitored using Time Domain Reflectometry equipment (Trase System I, Soil Moisture Equipment, Santa Barbara, CA).

**Aboveground Biomass**

Biomass harvests were carried out (1) at the beginning of the experiment in additional randomly chosen individuals (day 0, n = 10) and (2) at the end of experiment in both treatments (day 60, n = 10). In each species, harvested biomass was weighted after oven-drying for 72 h at 65°C. Biomass analysis did not include the root system; because of the very clayey soil and the size of the block used, it was not possible to separate it properly. Tolerance to flooding of the different species was determined through the calculation of the relative aboveground biomass after 60 d of flooding: \( \frac{(B_t - B_c)}{B_c} \), where \( B_t \) is mean aboveground biomass of flooded plants (excluding dead plants) and \( B_c \) is mean aboveground biomass of control plants.

**Root Porosity**

Sixty days after the beginning of the treatments, young roots of each species and individual replication were selected and root porosity was quantified using pycnometric techniques to estimate the root volume occupied by air (Sojka 1988). Root porosity (RP) was calculated as RP(%) = \( \frac{100 \times (P_G - P_R)}{(P + R - P_R)} \), where \( R \) is the fresh mass of intact roots (ca. 0.3 g), \( P_R \) is the pycnometer mass with water and intact roots, and \( P_G \) is the pycnometer mass with water and roots previously macerated with a mortar. The relative increase in root porosity for each species was calculated as \( \Delta Por = \frac{\left| (Por_F - Por_C) / Por_C \times 100 \right| }{\%} \), where \( Por_F \) is the mean root porosity of flooded plants and \( Por_C \) is the mean root porosity of control plants.

**Root Anatomy**

Samples of young roots 8–10 cm long were extracted from a soil depth of 0–5 cm from five individuals of each species and carefully washed and immediately fixed in formalin–acetic acid–alcohol (FAA) until processing for optical microscopy. Root sections (ca. 2 mm) from 2 cm from the tip were dehydrated and included in Spurr’s resin. Then, 1–2-μm cross sections were cut with an ultramicrotome and stained with potassium permanganate. For each species and individual replication, five sections were randomly selected and observed/photographed with an optical microscope (Zeiss Axioplan, Zeiss, Oberkochen, Germany) connected to an image analyzer (Imagenation Px, Imagenation, Beaverton, OR). In each section, root diameter and cortex thickness were measured, which allowed us to calculate the proportional contribution of cortex to root diameter.

**Table 2**

Aboveground Biomass of Plants Grown for 60 d under Control and Flooding Conditions

<table>
<thead>
<tr>
<th>Species</th>
<th>Aboveground biomass (g)</th>
<th>Day 0</th>
<th>Control</th>
<th>Day 60</th>
<th>Flooding</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Paspalidium paludivagum</em></td>
<td>2.8 ± 0.4</td>
<td>9.5 ± 1.2</td>
<td>10.4 ± 2.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Paspalum dilatatum</em></td>
<td>4.2 ± 0.6</td>
<td>38.9 ± 1.9</td>
<td>34.5 ± 3.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bothriochloa laguroides</em></td>
<td>2.1 ± 0.5</td>
<td>17.7 ± 3.7</td>
<td>2.8 ± 0.5*</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eryngium ebracteatum</em></td>
<td>0.5 ± 0.1</td>
<td>6.6 ± 1.0</td>
<td>5.3 ± 0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eclipta bellidioides</em></td>
<td>0.8 ± 0.2</td>
<td>4.5 ± 0.7</td>
<td>2.0 ± 0.5*</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Mentha pulegium</em></td>
<td>3.4 ± 0.3</td>
<td>30.9 ± 2.1</td>
<td>10.7 ± 1.7*</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Plantago lanceolata</em></td>
<td>1.6 ± 0.3</td>
<td>10.8 ± 1.7</td>
<td>3.1 ± 0.4*</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note. Values are means ± SE of 10 replications.

* Significant differences (\( P < 0.05 \)) among treatments at day 60 within each species based on Student’s *t*-test.
showed isolated circular lacunae positioned often in the outermost of the root cortex (fig. 2). In contrast, dicot species showed lysigenous lacunae arranged radially, separated by rows of intact or collapsed parenchymatic cells and occupying the lower increases in root porosity (fig. 1). The differential increase in the root porosity of each species, combined with the values of constitutive root porosity, resulted in a stronger positive correlation between final root porosity of the flooded plants and flooding tolerance of the different species ($r = 0.88; P < 0.01$) (fig. 1b).

Constitutive Root Traits

High values of constitutive root porosity were observed in all species, with the exception of B. laguroides, which presented the lowest porosity (7%) (fig. 1a).Dicot species presented similar values of constitutive root porosity of ca. 12%–14%, while the flood-tolerant grasses presented higher percentages of root porosity, reaching 23% in P. paludivagum and 32% for P. dilatatum (fig. 1a). In cross sections of control plant roots, all studied species showed some proportion of lysigenous constitutive aerenchyma (figs. 2, 3). Grasses showed lysigenous lacunae arranged radially, separated by rows of intact or collapsed parenchymatic cells and occupying most of the root cortex (fig. 2). In contrast, dicot species showed isolated circular lacunae positioned often in the outer section of the cortex. In the dicots E. ebracteatum and E. bellidioides, the proportion of lysigenous aerenchyma in the cortex was lower than in M. pulegium and P. lanceolata. Similar values of constitutive root porosity between both groups are explained mainly by the larger intercellular gas spaces in the first species (fig. 3a, 3c) and the development of secondary growth (with low porosity) in the second ones (fig. 3e, 3g). In spite of the young age of the roots, the species M. pulegium and P. lanceolata showed prominent secondary growth in all plants (fig. 3e, 3g); in contrast, E. ebracteatum and E. bellidioides showed slight or no secondary root growth (fig. 3a, 3c).

Changes in Root Anatomy Induced by Flooding

All species, again with exception of B. laguroides, showed significant increases ($n = 10, P < 0.05$) in the proportion of root porosity under flooding conditions (fig. 1b). Root porosity values reached by B. laguroides under flooding conditions...
were lower than 10%, compared to values over 20% recorded in the rest of the analyzed species (fig. 1b). Different patterns in the increase of root porosity were observed according to the species (figs. 2, 3). First, grasses *P. paludivagum* and *P. dilatatum* increased the proportion of root aerenchyma, which reached up to 40% in flooded plants, but showed only a small change in the number of lysed cells (fig. 2b, 2d). Additionally, a significant increase in the cortex proportion of the roots was recorded in both species (*n* = 10, *P* < 0.05), and in *P. paludivagum* the diameter of flooded roots was also greater (table 3). Second, dicot species *E. ebracteatum* and *E. bellidioides* (fig. 3b, 3d) increased the size of their lysigenous lacunae but maintained the cell layers adjacent to the stele. These species did not show changes (*n* = 10, *P* > 0.05) in the diameter or in the proportion of root cortex (table 3), and there was no evidence of secondary growth in flooded plants. Finally, the anatomical responses were very different in the species *M. pulegium* and *P. lanceolata* (fig. 3f, 3h), which showed lysigenous lacunae throughout their cortex in response to flooding. Moreover, in *M. pulegium* a significant increase (*n* = 10, *P* < 0.05) in root diameter in flooding conditions was recorded (table 3). In both species, secondary growth in flooded plants was markedly lower than in control plants (fig. 3f, 3h); therefore, a significant increase in the proportion of cortex in flooded roots was also recorded (table 3).

**Discussion**

**Root Porosity and Flooding Tolerance: Accounting Constitutive and Plastic Traits**

The results showed in all species the presence of extensive constitutive aerenchyma in the roots and significant increases...
in root porosity under flooding conditions, except in Bothriochloa laguroides, which did not present any of those characteristics. These traits are common in species inhabiting intermediate zones, which are known to tolerate both wet and dry soils (*sensu* Justin and Armstrong 1987). Such conditions also characterize the hydric regime of lowland communities in the flooding pampa grasslands (Burkart et al. 1990). The generation of aerenchyma tissue increases root porosity and aids the continuous conduction of air from the aerial parts to the roots (Laan et al. 1990), which is essential for

Fig. 3 Transverse sections of roots of *Eryngium ebracteatum* (a, b), *Eclipta bellidoides* (c, d), *Mentha pulegium* (e, f), and *Plantago lanceolata* (g, h) plants grown for 60 d under different treatments: control (*a, c, e, g*) and flooding (*b, d, f, h*). L = lysigenous aerenchyma. Bar = 45 μm.
survival in an environment with low oxygen in the soil (Armstrong 1979; Blom and Voesenek 1996). The overall analysis of the target species showed a consistent relationship between root porosity and flooding tolerance (fig. 1). This result concurs with other interspecific comparative studies, in which the lower or higher degree of tolerance to flooding was associated with a lower or higher constitutive porosity and/or with the plastic capacity to increase root porosity due to the generation of new aerenchyma tissue in the cortical parenchyma (Justin and Armstrong 1987; Visser et al. 1996; He et al. 1999).

Justin and Armstrong (1987) pointed out that the largest changes in root porosity are found in species with intermediate values under control conditions. Our results show complete agreement with these observations. Where constitutive root porosity is high, as in the tolerant grasses in our study, there is less potential for change. In this last situation, it was suggested that an increase in the porosity of the roots could be possible only if there were changes in root morphology (Justin and Armstrong 1987). Accordingly, the proportion of root porosity increased in native tolerant grasses, but there was a small change in the number of lysed cells (fig. 2), and the additional aerenchyma tissue was produced by increasing the diameter and, thereby, the cortex proportion of the roots (table 3). This response was also registered in the dicot Mentha pulegium and was previously reported for Rumex palustris (Engelaar and Blom 1995; Visser et al. 2000) and Juncus effusus (Visser et al. 2000); both species showed marked tolerance to soil anaerobiosis. However, in plants in which constitutive root porosity is low, as in the intolerant grass B. laguroides, there is probably an intrinsically low tolerance to flooding, and thus less adaptive plastic response to flooding could be expected. In the latter species, the constitutive low proportion of root cortex might play a key factor in explaining poor aeration and low tolerance during flooding conditions (McDonald et al. 2002).

It was pointed out that the ventilating potential of tissues would benefit more from cell cubic configurations than from hexagonal arrays and also that closer packing and early secondary growth would diminish gas diffusion (Kawase 1981; Justin and Armstrong 1987). In this way, a lag in secondary growth during flooding was detected in both groups of dicots, which is a common characteristic of many dicot species tolerant to flooding (Justin and Armstrong 1987; Jackson and Armstrong 1999). Moreover, dicot species showed similar amounts of root porosity, but the arrangement of cortical aerenchyma induced by flooding conditions differs greatly from species to species (fig. 3). Mentha pulegium and Plantago lanceolata showed lysigenous aerenchyma throughout their cortex. In contrast, the species Eryngium ebracteatum and Eclipta bellidioides increased the size of their lysigenous lacunae but maintained intact the cell layers adjacent to the stele. It would seem that these latter species (fig. 3b, 3d), in which at least part of the cortex remained intact, and the native grasses (fig. 2b, 2d), which have sclerenchymatic cells in the outer layer of the cortex (Smirnoff and Crawford 1983; Vasellati et al. 2001), could have attained high values of root porosity without losing mechanical resistance. This property is known to be useful to resist soil compaction under natural conditions (Engelaar and Blom 1995), particularly relevant when one considers the possibility of direct trampling by cattle or when soil shrinkage during summer increases soil bulk density of these grasslands (Taboada and Lavado 1993). Experimental studies to test whether anatomical responses to flooding result in different root structural resistances between the different groups of species merit further investigation.

Ecological Significance and Field Observations Associated with Flood-Tolerance Traits

Flooding conditions did not affect (or affected only to a small extent) aboveground biomass of the species Paspalium paludivagum, Paspalum dilatatum, and E. ebracteatum, which showed high values of root porosity (table 2). In a second group, individuals of the species E. bellidioides, M. pulegium, and P. lanceolata continued growing and survived the flooding, but marked differences were found between aboveground biomass compared to nonflooded plants (table 2). The presence of constitutive traits and the intermediate values of flooding-induced root porosity found in the less tolerant dicot species could at least explain the vegetative survival of these species under natural flooding conditions. Finally, individuals of B. laguroides, which did not show significant anatomical traits associated with flooding tolerance, were severely affected by this disturbance in their aboveground biomass. At field conditions, the less tolerant dicot species and the grass B. laguroides would recover their presence and recolonize the site only if flooding periods are less frequent and less intensive. This process is one of the major

Table 3

<table>
<thead>
<tr>
<th>Root Diameter and Proportion of Cortex of Plants Grown for 60 d under Control and Flooding Conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Root Diameter (μm)</strong></td>
</tr>
<tr>
<td><strong>Control</strong></td>
</tr>
<tr>
<td>Paspalium paludivagum</td>
</tr>
<tr>
<td>Paspalum dilatatum</td>
</tr>
<tr>
<td>Bothriochloa laguroides</td>
</tr>
<tr>
<td>Eryngium ebracteatum</td>
</tr>
<tr>
<td>Eclipta bellidioides</td>
</tr>
<tr>
<td>Mentha pulegium</td>
</tr>
<tr>
<td>Plantago lanceolata</td>
</tr>
</tbody>
</table>

Note. Values are means ± SE of five replications.
* Significant differences (P < 0.05) among treatments within each species based on Student’s t-test.
registered fluctuations of the plant community in these grasslands. The high correlation between root porosity and tolerance to flooding of the different species matched the species range tolerance observed in previous reports on natural flooding in the field (Insausti and Soriano 1987; Chaneton et al. 1998; Burkart et al. 1990; Insausti et al. 1999), indicating that constitutive tolerance, as well as the different plastic responses associated with flooding, would strongly influence the performance and abundance of species coexisting in the same plant community (Van der Sman et al. 1988, 1993).

At the community level, Insausti et al. (1999) pointed out that harmful effects of soil anaerobiosis on intolerant species in addition to the simultaneous increase in the availability of scarce nutrients (e.g., phosphorus) during flooding (Rubio et al. 1997), could provoke a relaxation of the competitive interactions that favor the most tolerant species to a greater extent. This idea would be supported by our results, since we found no differences in the biomass of tolerant species between flooded and control plants (at the individual plant extent. This idea would be supported by our results, since we found no differences in the biomass of tolerant species between flooded and control plants (at the individual plant level with less neighborhood competition); however, great positive differences in aboveground biomass were found by these authors when these species cohabited with other flooding-intolerant species of the grassland (community level).

Plastic responses related to flood tolerance could minimize some deleterious effects of anaerobiosis but also maximize any environmental positive effect (Bradshaw 1965; Via et al. 1995). The use of vacant resources by tolerant species would give an ecological significance to the differential tolerance to flooding of the competing species of these grasslands (Crawford et al. 1989; Insausti et al. 1999).

**Acknowledgments**

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