

PHYSIOLOGICAL AND MORPHOLOGICAL RESPONSES OF *BRACHIARIA* SPP. TO FLOODING¹

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ABSTRACT - The physiological and morphological responses of the forage grasses *Brachiaria brizantha* cv. Marandu, *B. decumbens* and *B. humidicola* were compared for plants grown in pots under flooding and well-drained conditions for 14 days. Flooding reduced specific leaf area and biomass allocation to roots in all species and enhanced leaf senescence in *B. brizantha* and *B. decumbens*. Relative growth rate was reduced by flooding in *B. brizantha* and *B. decumbens*, but not in *B. humidicola*. Leaf elongation rate was unaffected by flooding in *B. decumbens* and *B. humidicola*, but declined in *B. brizantha* since the first day of flooding. Net photosynthesis and leaf chlorophyll content were reduced by flooding in *B. brizantha*; however, no flooding effect could be detected in the other two species. For all species, there was a close relationship between net photosynthesis and stomatal conductance under flooding. These results show that the studied species have distinct degrees of tolerance to flood, *B. brizantha* is intolerant, *B. decumbens* is moderately tolerant and *B. humidicola* is tolerant. Because leaf elongation rate was immediately depressed by flooding only in *B. brizantha*, this measurement could be appropriate as an early detection mechanism for relative flood tolerance in *Brachiaria* spp.

Index terms: *Brachiaria brizantha*, *Brachiaria decumbens*, *Brachiaria humidicola*, leaf area, chlorophyll, photosynthesis, biomass, growth rate.

RESPOSTAS MORFOLÓGICAS E FISIOLÓGICAS DE *BRACHIARIA* SPP. AO ALAGAMENTO DO SOLO

RESUMO - As respostas morfológicas e fisiológicas de *Brachiaria brizantha* cv. Marandu, *B. decumbens* e *B. humidicola* foram comparadas em plantas cultivadas em vasos, sob solo alagado e bem drenado durante 14 dias. O alagamento reduziu a área foliar específica e a alocação de biomassa para as raízes em todas as três espécies e aumentou a senescência foliar em *B. brizantha* e *B. decumbens*. O alagamento reduziu a taxa de crescimento relativo em *B. brizantha* e *B. decumbens*, mas não em *B. humidicola*. A taxa de elongação foliar não foi afetada pelo alagamento em *B. decumbens* e *B. humidicola*, mas diminuiu em *B. brizantha* desde o primeiro dia de alagamento. A fotossíntese líquida e o conteúdo de clorofila foliar foram reduzidos pelo alagamento em *B. brizantha*; no entanto, nenhum efeito do alagamento pôde ser detectado nas outras espécies. Em todas as espécies, existiu uma estreita relação entre as taxas de fotossíntese líquida e a condutância estomatal. Esses resultados mostram que as espécies estudadas diferem quanto à tolerância ao alagamento. *B. brizantha* é intolerante, *B. decumbens* é moderadamente tolerante e *B. humidicola* é tolerante. Em virtude de a taxa de elongação foliar ter sido imediatamente afetada somente em *B. brizantha*, este parâmetro pode ser empregado como um mecanismo de detecção prematura da tolerância ao alagamento em *Brachiaria* spp.

Termos para indexação: *Brachiaria brizantha*, *Brachiaria decumbens*, *Brachiaria humidicola*, área foliar, clorofila, fotossíntese, biomassa, taxa de crescimento.

INTRODUCTION

Many key physiological and morphological processes in plants like carbon assimilation and allocation are greatly influenced by environmental stresses (Field, 1991; Geiger & Servaites, 1991). The nature of these responses is dependent on the acclimation

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capacity (plasticity) of the plant. This plasticity dictates the species' ability to maximize resource acquisition under adverse conditions. There is very little published information on the physiological responses of tropical forage grasses to environmental stresses, particularly to flooding or waterlogging (Humphreys, 1980; Medina & Motta, 1990; Baruch, 1994a, 1994b). This information is important to understand the physiological mechanisms involved in stress tolerance or susceptibility, help predict their productive potential under certain environmental conditions, and ultimately, provide the needed information to manage pastures successfully.

Temporary or continuous flooding of soils occurs as a result of storms, overflowing of rivers, or inadequate drainage. Because in some tropical regions pasture areas are usually located in marginal areas, not suited for agriculture, pastures can be intermittently affected by flooding or waterlogging. In such areas, flood-tolerant grasses would have a greater advantage over less tolerant ones.

Forage grasses of the genus *Brachiaria* are of growing importance in the tropics and particularly in Brazil (Argel & Keller-Grein, 1996). Throughout tropical America *B. brizantha* (Hochst. ex A. Rich.) Stapf cv. Marandu, *B. decumbens* Stapf and *B. humidicola* (Rendle) Schweick are the most important species of this genus. Although there is a great deal of information, particularly in the gray literature, describing the relative tolerance of these species to flooding or waterlogging, this information is usually based on anecdotal evidence. There is no comparative study examining the physiological and morphological responses of these species under flooding.

The objectives of this study were to investigate the effects of flooding on key physiological and morphological responses in *B. brizantha*, *B. decumbens* and *B. humidicola* and to relate these responses to the species' flood tolerance.

MATERIAL AND METHODS

Plant materials and growing conditions

Seeds of *Brachiaria brizantha* (Hochst. ex A. Rich.) Stapf cv. Marandu, *B. decumbens* Stapf and *B. humidicola* (Rendle) Schweick were germinated on sand and then planted individually in pots with 2 kg (dry weight) of soil

(1:1; organic soil to sand). Prior to planting, pots were fertilized with a solution of 40 mg of P (K_2HPO_4) per kg of soil. Plants were grown outdoors for the duration of the experiment under a shade net that intercepted ca. 50% of direct solar radiation. Each pot was watered daily and fertilized every other day, until imposition of flooding with 5 mL of a water soluble fertilizer solution (15:30:15; N:P₂O₅:K₂O; 1 g L⁻¹). Flooding was imposed 21 days after planting by inundating the pots up to 3 cm above the soil level and control pots were free-draining and watered daily. Flooding lasted 14 days for all species. All species remained vegetative during the experimental period.

Gas exchange

Net photosynthesis (A) and abaxial stomatal conductance to water vapor of intact leaves were measured with a portable photosynthesis system (LI-6200, Li-Cor, inc., Lincoln, NE, USA) and a diffusion porometer (AP4, Delta T Devices, Cambridge, UK). Measurements were made 120 hours before the end of the experiment, on one young, fully expanded blade of a vegetative tiller on each plant. Gas exchange parameters were calculated on a leaf area basis. Photosynthesis measurements were made outdoors on a sunny, cloudless day, between 11h and 12h local time, with a PPFD of $1752 \pm 14 \mu\text{mol m}^{-2} \text{s}^{-1}$ (mean \pm s.e.). Stomatal conductance measurements were made on three occasions, 9, 11 and 14h local time, on the same leaves used for photosynthesis measurements.

Growth analysis

Three harvests were made; the first harvest was on the day flooding treatment was imposed (ca. 25 days after germination), and the others seven and 14 days later (n = 7 per harvest and treatment). At each harvest, plant material was divided into leaf blades, culms (sheath and stem), roots and dead leaf tissue. Leaf blades were removed and their areas were measured using a leaf area meter (LI-3000, with conveyor belt assembly, LI-3050; Li-Cor, Inc., Lincoln, NE, USA). Roots were washed free of soil using a manually manipulated jet spray of water. Plant dry mass was obtained by drying the plant material at 65°C for 48 hours. At each harvest, the specific leaf area (leaf area per unit of leaf dry mass, SLA) and leaf, culm, root and dead leaf tissue mass ratios (respectively, leaf, culm, root and dead leaf tissue dry mass per unit of dry mass of whole plant, leaf mass ratio (LMR), culm mass ratio (CMR), root mass ratio (RMR) and dead leaf tissue mass ratio (DMR) were calculated according to Hunt (1990). Relative growth rate (change in total dry mass per total dry mass of plant per day, RGR) was also calculated for each harvest interval.

Leaf elongation rate

The length of a young expanding leaf blade (with the ligule not yet exposed) of a vegetative tiller of each plant was measured with a ruler at around the same time every day. Leaves being measured were marked with a plastic ring. Once the ligule was exposed, a new leaf, on the same plant, was marked and measured. Daily leaf elongation was calculated as the difference between leaf lengths of two consecutive days.

Leaf chlorophyll content

Parts of the leaf blades used for gas exchange measurements were processed for chlorophyll content following the method described by Arnon (1949).

Experimental design and statistical analysis

The plastic containers were arranged in a completely randomized design with seven replications. For the leaf elongation measurements four replications were used, while for photosynthesis, stomatal conductance, and leaf chlorophyll content, three replications were used. Differences in net photosynthesis, and leaf chlorophyll content were assessed by two-way analyses of variance (ANOVA) with treatments (control and flooding) and species (*B. brizantha*, *B. decumbens* and *B. humidicola*) as main effects. Differences in biomass allocation, specific leaf area (SLA) and leaf elongation throughout the experimental period were assessed by three-way ANOVA with treatments, species and evaluation dates as main effects. The assumption of homogeneity of variances and normality were tested for each ANOVA and when necessary data were log transformed. Transformed values were back transformed for presentation. *Post hoc* contrasts were calculated for assessing differences between treatments or within days and between treatments whenever appropriate.

Stomatal conductance data were analyzed by ANOVA with repeated measures (Von Ende, 1993). The between-subject main effects were species and treatments and the within-subject or repeated measures effect was time of measurement. Homoscedastic residuals were obtained with log-transformed values of stomatal conductance (Box M test, $P = 0.13$). Compound symmetry of the covariance matrix was confirmed by the Mauchly's sphericity test ($P = 0.55$). The Huynh-Feldt corrected significance levels were considered for the analysis.

The statistical package STATISTICA for Windows release 5.0 (Statistica for Windows, 1994) was used for all computations of the data.

RESULTS AND DISCUSSION

Biomass allocation and growth

The ANOVA revealed a significant species x treatment interaction effect for the proportion of biomass allocated to roots (RMR), leaves (LMR), culms (CMR) and dead leaf tissue (DMR) ($F_{2, 108} \geq 3.18$; $P \leq 0.045$). For all species flooding significantly decreased RMR (*post hoc* contrasts, $F_{1, 108} \geq 73.1$; $P < 0.0001$). This effect, however, was greater in *B. brizantha* and lower in *B. humidicola* (Table 1). For LMR, no significant difference between treatments could be detected for *B. decumbens* ($F_{1, 108} = 3.31$; $P = 0.08$). For *B. brizantha* and *B. humidicola* a significantly ($F_{1, 108} \geq 6.34$; $P \leq 0.01$) greater proportion of carbon was allocated to leaves in flooded plants (Table 1). Flooding also promoted a greater ($P < 0.0001$) allocation of biomass to culms in all species, and increased ($P \leq 0.001$) the proportion of dead leaf tissue (i.e. leaf senescence) in *B. decumbens* and *B. brizantha* (Table 1).

A reduction in resource allocation from below- to above-ground components is a common response of plants to transient flooding or waterlogging (Yamamoto et al., 1995). Even in flood-tolerant grasses this response is typical (Naidoo & Naidoo, 1992; Naidoo & Mundree, 1993; Baruch, 1994a; Loreti & Oosterheld, 1996). The reason for that is because, in general, anoxia is fatal to all roots, even in anoxia tolerant species (Crawford & Braendle, 1996). As reviewed by Kozłowski (1997), flooding induces root decay, affects root formation and branching, and growth of existing roots. However, the mechanisms of root acclimation to anoxia differ according to the flood tolerance of the plant species (Drew, 1997).

For specific leaf area (SLA) the highest order interaction was significant ($F_{4, 108} = 2.52$; $P = 0.045$). *Post hoc* contrasts showed that both at seven and at 14 days all species had significantly lower SLA in the flooded treatment (Fig. 1) ($F_{1, 108} \geq 4.2$; $P < 0.04$). Mean SLA for the entire experiment was 11% lower ($P < 0.001$) in flooded *B. decumbens* and *B. humidicola* and 7% lower ($P = 0.01$) in flooded *B. brizantha*.

Because variations in SLA can be determined by leaf chemical characteristics such as starch accumu-

lation (Lambers & Poorter, 1992) which is known to occur in flooded plants (Liao & Lin, 1994; Gravatt & Kirby, 1998), it is possible that a reduction in the translocation of photosynthates from leaves to various sinks in the studied species was the major cause for the measured SLA values.

The ANOVA for relative growth rate (RGR) also showed a significant highest order interaction ($F_{2,66} = 7.76$; $P < 0.001$). *Post hoc* contrasts for the species x treatment interaction showed that both *B. brizantha* and *B. decumbens* had their RGR significantly reduced by flooding ($F_{1,66} \geq 13.8$; $P < 0.001$) (Fig. 2). No significant difference between treatments could be detected for *B. humidicola* ($F_{1,66} = 3.68$; $P = 0.06$), although there was a tendency for reduced RGR in flooded plants (Fig. 2). Relative growth rate was positively related to the overall response of the three species to flooding, where *B. brizantha* was highly sensitive and *B. humidicola* less sensitive.

Leaf elongation rate

A significant species x treatment interaction was detected for leaf elongation ($F_{2,234} = 12.8$; $P < 0.0001$) (Fig. 3). Differences between treatments, within the same species, assessed by *post hoc* contrasts indicated that the mean leaf elongation for the entire experiment in *B. brizantha* was significantly ($F_{1,234} = 32.5$; $P < 0.0001$) reduced by flooding, while no difference between treatments could be detected

for *B. decumbens* and *B. humidicola* ($P \geq 0.43$) (Fig. 3).

A decrease in leaf elongation in flooded soil is usually correlated to lower flooding tolerance in grass species or cultivars (Lizaso & Ritchie, 1997; Yamaguchi & Biswas, 1997). The immediate decrease (day one) in leaf elongation rate and the significantly lower mean leaf elongation for the entire experimental period of *B. brizantha* can be attributed to its greater sensitivity to flooding stress. On the other hand, based on their daily leaf elongation response, both *B. humidicola* and *B. decumbens* showed similar degree of sensitivity to flooding, with no immediate change in leaf elongation patterns. Because forage production in grasses can be highly dependent on elongation of existing leaves (Skinner & Nelson, 1994) and a higher leaf elongation in flooded grasses can be important for O_2 access of submerged leaves, it could be speculated that both *B. humidicola* and *B. decumbens* have a greater ability to cope with flooding stress when compared to *B. brizantha*.

Leaf chlorophyll content

Total leaf chlorophyll content was negatively affected by flooding in *B. brizantha* ($F_{1,12} = 5.75$; $P = 0.03$). No significant treatment effect could be detected for *B. decumbens* and *B. humidicola* (Fig. 4).

TABLE 1. Leaf mass ratio (LMR, kg kg⁻¹), culm mass ratio (CMR, kg kg⁻¹), root mass ratio (RMR, kg kg⁻¹) and dead leaf tissue mass ratio (DMR, kg kg⁻¹), as means of the entire experiment, of *B. brizantha*, *B. decumbens* and *B. humidicola* under flooding and control treatments. Values are means (\pm s.e.), $n = 21$. For each species, significance between means within columns is given by * <0.01 , ** <0.001 and ns = $P > 0.05$ (*post hoc* contrasts).

Treatment	LMR	CMR	RMR	DMR
<i>B. brizantha</i>				
Control	0.34 (0.01)*	0.28 (0.01)**	0.37 (0.013)**	0.01 (0.002)**
Flooding	0.40 (0.01)	0.36 (0.01)	0.21 (0.018)	0.02 (0.01)
<i>B. decumbens</i>				
Control	0.33 (0.01) ^{ns}	0.32 (0.01)**	0.35 (0.01)**	0.004 (0.001)**
Flooding	0.35 (0.01)	0.39 (0.01)	0.22 (0.02)	0.041 (0.01)
<i>B. humidicola</i>				
Control	0.30 (0.02)*	0.33 (0.01)**	0.36 (0.02)**	0.002 (0.001) ^{ns}
Flooding	0.33 (0.02)	0.42 (0.02)	0.25 (0.01)	0.006 (0.002)

The ability to keep leaf chlorophyll levels under flooding or waterlogging is considered a tolerance mechanism in grass species (Baruah, 1996; Sarkar et al., 1996). An increased leaf chlorosis and leaf senescence are common responses in flood-intolerant species (Pezeshki, 1994). In the present study, for both *B. brizantha* and *B. humidicola* there was a close relationship among chlorophyll content, photosynthetic response and leaf senescence, reflecting the different degree of tolerance to flooding of these species. For *B. decumbens*, this relationship was less evident

due to the high degree of premature leaf senescence observed in flooded plants.

CO₂ assimilation

Net photosynthesis in *B. brizantha* was reduced 89% by flooding ($F_{1,12} = 19.5$; $P < 0.001$) (Fig. 5). In *B. decumbens* there was a tendency for lower photosynthesis in flooded plants, however, this difference was not statistically significant ($P = 0.07$). No significant difference between treatments could be detected in *B. humidicola* ($P = 0.9$) (Fig. 5).

Net photosynthesis is known to be drastically reduced in flood-sensitive plants (Pezeshki, 1994). For example, net photosynthesis rates of both flood-tolerant and flood-intolerant tree seedlings species were significantly reduced by flooding, however, this reduction was higher for flood intolerant species (Gravatt & Kirby, 1998). The same tendency was observed in two wheat genotypes by Huang et al. (1994), in *Phaseolus vulgaris* cultivars by Lakitan et al. (1992) and in two weed species of *Ipomoea* by Gealy (1998). On the other hand, flooding caused no significant net photosynthesis reduction in the flood-tolerant tropical grasses *Echinochloa polystachya* (Baruch, 1994b; Piedade et al., 1994) and *B. mutica* (Baruch, 1994b). In the present study, based on their overall response, *B. brizantha* proved to be highly sensitive to flooding while *B. humidicola* and, to some extent, *B. decumbens* were relatively more tolerant.

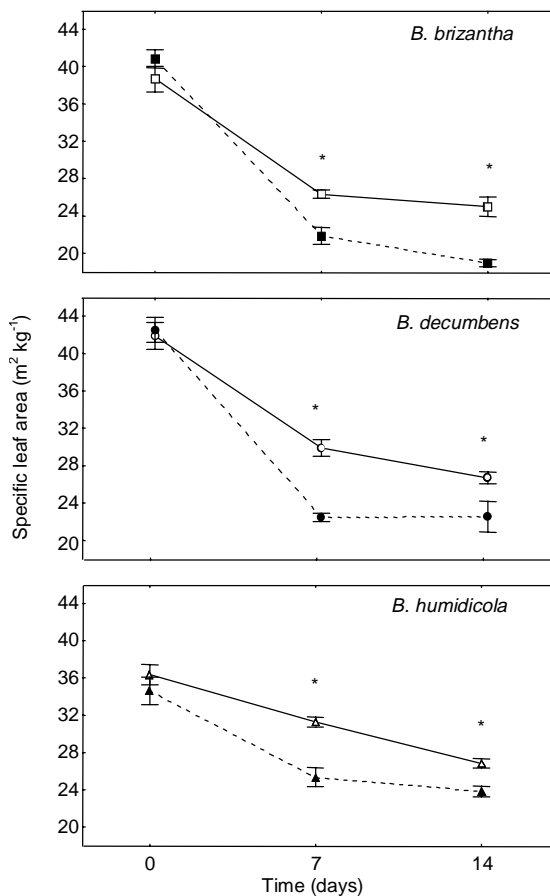


FIG. 1. Specific leaf area of *Brachiaria* spp. under flooding (closed symbols, dashed line) and controlled (open symbols, solid line) conditions. Each point represents the mean \pm s.e. ($n = 7$). An asterisk indicates a significant difference (*post hoc* contrasts; $P < 0.05$) within each species and day.

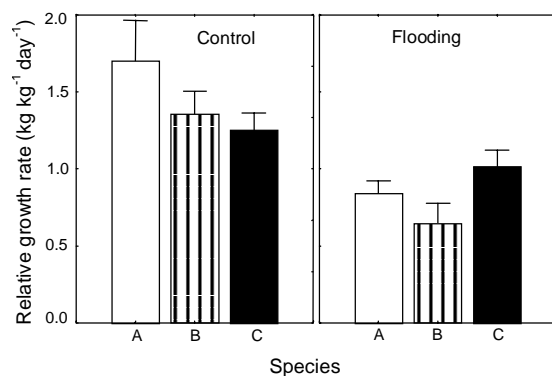


FIG. 2. Relative growth rate of *Brachiaria* spp. under flooding and controlled conditions. Data are means \pm s.e. ($n = 21$). A = *B. brizantha*, B = *B. decumbens* and C = *B. humidicola*.

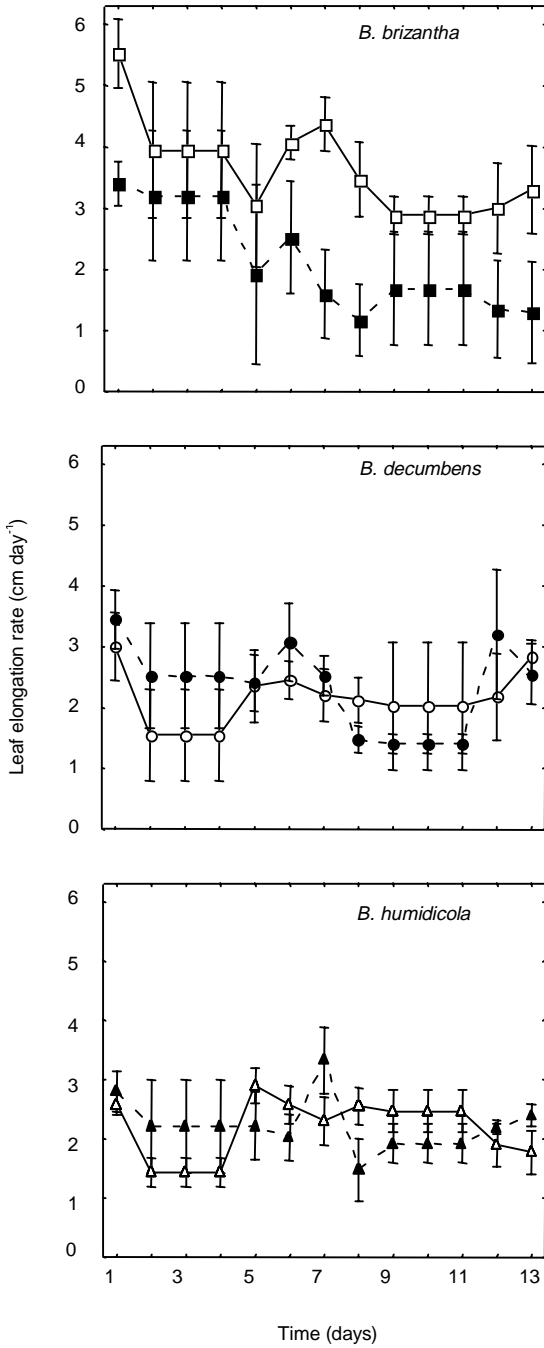


FIG. 3. Leaf elongation rate of *Brachiaria* spp. under flooding (closed symbols, dashed line) and controlled (open symbols, solid line) conditions. Each point represents the mean \pm s.e. (n = 4).

Leaf conductance

There was no within subjects significance in the repeated measures ANOVA for stomatal conductance. However, the effects of species ($F_{2, 18} = 6.35$; $P = 0.008$) and treatment ($F_{1, 18} = 5.02$; $P = 0.03$) were significant in the between-subjects effects. *Brachiarium humidicola* had the highest mean stomatal opening (0.164 vs. 0.091 and 0.092 mol m⁻² s⁻¹ for *B. decumbens* and *B. brizantha*) and flooding reduced by 27% the mean leaf conductance of the three species (0.134 vs. 0.098 mol m⁻² s⁻¹). This reduction was

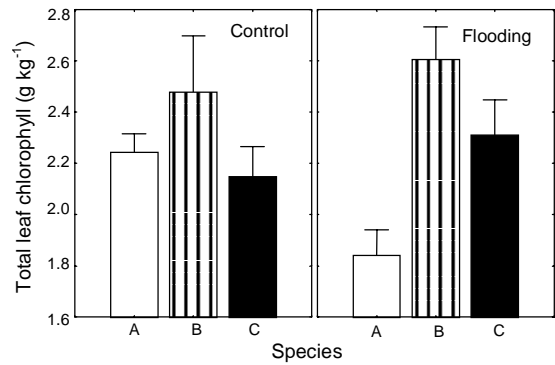


FIG. 4. Total leaf chlorophyll content of *Brachiarium* spp. under flooding and controlled conditions. Data are means \pm s.e. (n = 3). A = *B. brizantha*, B = *B. decumbens* and C = *B. humidicola*.

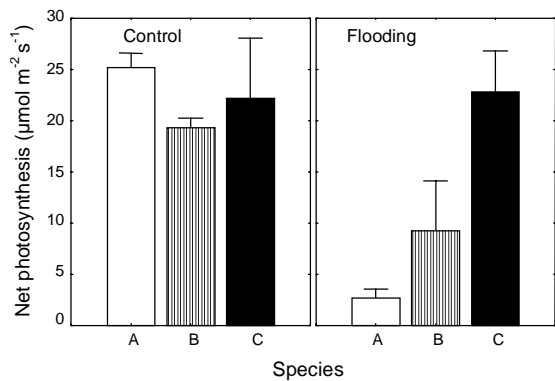


FIG. 5. Net photosynthesis of *Brachiarium* spp. under flooding and controlled conditions. Data are means \pm s.e. (n = 3). A = *B. brizantha*, B = *B. decumbens* and C = *B. humidicola*.

higher in *B. brizantha* (29%) and lower in *B. humidicola* (4%).

Stomatal conductance is usually reduced by flooding (Liao & Lin, 1994; Huang et al., 1995). In the present work, a close relationship between stomatal conductance and CO₂ assimilation was observed in the three species. This response indicates that net photosynthesis was influenced primarily by stomatal conductance. A similar stomatal response among flood-tolerant and flood-intolerant grass species was also reported by Baruch (1994b).

CONCLUSIONS

1. *Brachiaria brizantha* is apparently flood-intolerant, *B. decumbens* moderately flood-tolerant and *B. humidicola* is flood-tolerant.

2. Net photosynthesis, stomatal conductance, relative growth rate, biomass allocation to roots and leaf elongation rate in the flooded *Brachiaria* spp. are directly related to their ability to tolerate flooding.

3. Because leaf elongation rate was immediately (day one) depressed in the flood-intolerant *B. brizantha*, and no apparent effect of flooding could be detected for the more tolerant *B. humidicola* and *B. decumbens*, this non-destructive and non-invasive measurement can be used as an early detection mechanism of relative flood tolerance in *Brachiaria* spp.

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