Chapter 22
Competition Alters Responses of Juvenile Woody Plants and Grasses to Nitrogen Addition in Brazilian Savanna (Cerrado)

Viviane T. Miranda, Mercedes M. C. Bustamante and Alessandra R. Kozovits

Abstract The Cerrado, Brazilian savanna, is characterized by high radiation and dystrophic soils. Seedlings of woody species must compete effectively for resources belowground in order to establish in the herbaceous matrix. Few studies focus on the dynamics of herbaceous and woody juvenile plants and their competitive strategies, especially under increasing nitrogen (N) availability. In the present study, seedlings of three woody species, *Eugenia dysenterica, Magonia pubescens* and *Enterolobium gummiferum* were grown with or without the dominant grass in Cerrado areas of central Brazil, *Echinolaena inflexa*. Half of the pots were exposed to N additions equivalent to a deposition of 20 kg N-NO_3NH_4 ha^{-1} $year^{-1}$. The N induced responses of plants growing under intra and interspecific competition were analyzed, with special attention to plasticity of root biomass and morphology. One year after the beginning of the experiment, the fresh and dry biomass of roots and shoots were weighted. Before drying, total length, surface area and diameter of roots were determined. Interspecific competition tended to reduce root and shoot biomass of all plants. However, effects of competition with *E. inflexa* were more obvious on root morphology, being total root and fine root length diminished in two of the woody species in the absence of N addition. The enhancement of N availability, in general, minimized the effects of competition, increasing the potential competitiveness of some woody species due to changes in total fine root length

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and biomass. The results provide indication that competition between saplings of woody plants and grasses could be an important factor driving plant allometry and morphology during the first stages of development in Cerrado environments. The responsiveness of plants to N deposition seemed to depend, in part, on the type of competition (intra- or interspecific), what should be taken into account in models of vegetation dynamics in response to nutrient deposition.

Keywords Native savannah plant species • Nitrogen deposition • Root morphology • Sapling growth • Woody plant and grass competition

22.1 Introduction

Savanna ecosystems are characterized by the coexistence of a shrub-tree layer and a grass layer. In Brazil, about 2,000,000 km^2 of land was originally occupied by the Brazilian savanna (Cerrado), although large areas have already been converted into pastures and agricultural fields. Integrated in the herbaceous matrix, seedlings of woody species must compete effectively for resources in order to establish. The Cerrados are characterized by high radiation and dystrophic soils. Below-ground competition for nutrients appears to play a major role in community structure compared with competition aboveground. Plasticity in root morphology and physiology might therefore be important traits, hitherto little researched in such ecosystems (Grams and Andersen 2007). Despite the obvious importance of the undergrowth layer in grassland areas of the Cerrado, few studies focus on the dynamics of herbaceous and woody juvenile plants and their competitive strategies. Changes in the distribution of these plant life forms due to differential responses to variations in nutrient availability might have several consequences that affect ecosystem function.

In the last century, native ecosystems have been involuntarily fertilized with nitrogen from atmospheric deposition. It is estimated that the deposition of nitrogen (N) has increased by about 4.5 times from 1843 to the present (Goulding et al. 1998), and will continue to rise due to the expansion of pasture and nitrogen-fixing crop legumes, increased use of N fertilizers, burning of plant biomass and industrial activities (Vitousek et al. 1997). The main N forms emitted by human activities (NO, N_2O, NH_3, NO_2) and their products of reaction (NH_4^+, NO_3^- and HNO_3) are highly mobile in the atmosphere and can be deposited hundreds of miles from their sources (Asman et al. 1998; Fabian et al. 2005). Thus, the dichotomy between anthropogenically altered ecosystems and wild areas, free of human influence, begins to fade.

The enhancement of N availability for vegetation can cause increases in N concentration in plant tissues and reduce C:N ratios, increase foliar N:P ratios, change biomass allocation to shoots or to storage organs, reduce scleromorphy features e.g. low specific leaf area and increase photosynthetic rates of all species (Harmens et al. 2000; Zak et al. 2000) and thus, alter the competitiveness of different species. In the northern hemisphere, changes in structure and composition of plant communities as a function of elevated atmospheric N deposition have been observed, with an increase in nitrophilous species at the expense of N sensitive species (Bobbink et al. 1998).

In an N addition experiment in native Brazilian savanna (Cerrado), grasses responded rapidly to fertilization, increasing their biomass, whereas dicotyledons did not respond to fertilization. Comparing different grasses, a C_3 species was favoured over diverse C_4 species (Luedemann 2001), especially under the combination of N and phosphorus (P) fertilization. Considering the tree layer, the increased N availability alone or in combination with P amendment led to higher stem relative growth rates (Simpson 2002), higher concentrations of leaf N, reduced N resorption rate during senescence and acceleration of leaf litter decomposition at the community level (Kozovits et al. 2007). However, the magnitude of these responses varied widely between species and there were no information about root responses. The consequences of long-term changes in the ecophysiology of individual species and of functional groups of plants to the structure and composition of the community of Cerrado are still unknown. It is especially unclear how the seedlings of woody species and grasses, coexisting in the understory layer, will respond to increased N availability, and how these responses will affect the relative competitive ability of these two plant functional groups.

The objective of this study was to evaluate N induced responses of juvenile woody plants and the dominant C_3 grass in Cerrado areas of central Brazil, growing under intra and interspecific competition. Special attention was given to responses involved in competition, in terms of root biomass and morphology.

22.2 Methodology

The experiment was conducted under greenhouse conditions at the Experimental Station of the University of Brasília, Brasília, Brazil. Seeds of native Cerrado woody plants, including two non-leguminous—*Eugenia dysenterica* (Myrtaceae) and *Magonia pubescens* (Sapindaceae) and a legume species, *Enterolobium gummiferum* (Leguminosae-Mimosoideae) were germinated in agar.

About 20 days after germination, the seedlings were transferred to plastic bags filled with a mixture of Cerrado soil and washed sand (2:1 ratio), and were taken to the greenhouse to acclimate. Within ~30 days, the seedlings were transplanted into 18 L polyethylene pots filled the same substrate described above. The mixture of soil and sand was added over a layer of gravel for better drainage. Three individuals of the same species of woody plants were placed in each pot to grow in the absence of grass (intraspecific competition) or in the presence of grass (see below, interspecific competition) in February 2008.

Rhizomes of the C_3 grass *Echinolaena inflexa* were collected in natural field sites close to Brasília, selected by similar size and transplanted into pots. Each pot received two to four rhizome parts for a total of approximately 5 g fresh biomass per pot. Seventy pots were prepared, 20 for each species of woody plants (10 in monoculture and 10 in mixed culture with grass) and 10 for the grass monoculture.

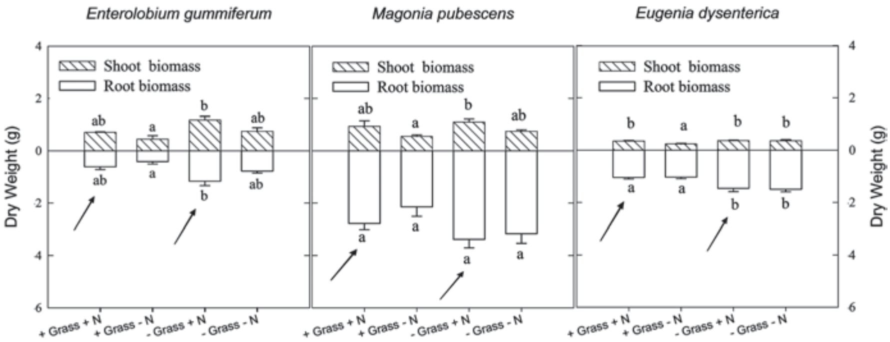

Fig. 22.1 Dry weight of shoots and roots of three woody species growing in monoculture (−Grass) and in the presence of grass (Grass+), without (−N) and with (+N) fertilization. Different letters indicate significant differences among treatments ($p<0.05$). *Arrows* ↑ indicate treatments with N addition

To determine the effect of enhanced N availability on sapling development and on their competitive abilities, half of the pots received addition of 0.0171 g of N in the form of NO_3NH_4, divided into five monthly applications (from September 2008 to January 2009), amount equivalent to a deposition of 20 kg N ha^{-1} $year^{-1}$. Fertilizer was dissolved in distilled water and applied over the soil. The pots were randomly divided between three benches in the greenhouse at the Experimental Station Biological UnB and rotated every 20 days throughout the experimental period.

Five months after transplanting to pots, plants presented yellowish spots on the leaves indicating nutrient deficiency. Thus, Hoagland solution was applied (1/2 strength in the first two applications and 1/3 strength in the last two). 45 ml of nutrient solution were applied per pot every two weeks between July and August 2008.

One year after, the individuals were collected the fresh and dry biomass (after drying at 60 °C for 48 h) of root, shoot non-photosynthetic (stem and branches) and leaves were determined. Grasses were also collected and weighed separately as roots and shoots. Before drying, the root system of each individual was scanned (Epson Perfection V700 Photo) and the images analyzed with the software WinRhizo 2008a for determination of the total length, surface area, mean diameter and length of fine roots (up to 0.5 mm in diameter).

Data distribution was tested by Kolmogorov–Smirnov test. Differences between means were tested by ANOVA< and post-hoc test and were considered significant at $p<0.05$.

22.3 Results and Discussion

Interspecific competition tended to reduce root and shoot biomass of juvenile woody plants and grasses (Figs. 22.1 and 22.2). However, significant effects were found, mainly, on root length (Fig. 22.3). The higher N availability minimized the nega-

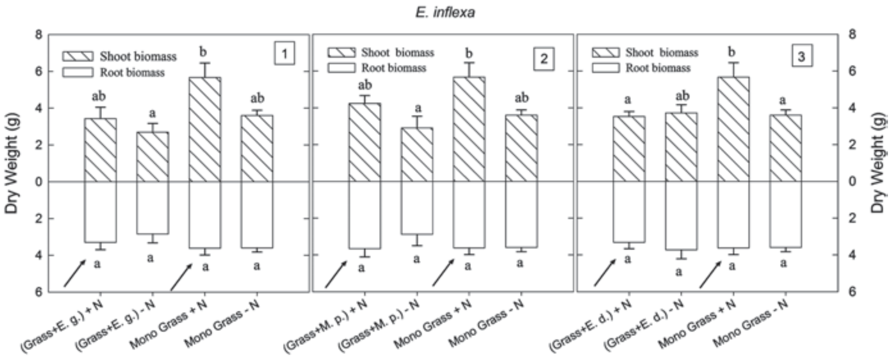

Fig. 22.2 Dry weight of shoot and root system of the grass *E. inflexa* in monoculture (mono. Grass) and in competition with woody species, (*1*) grass + *E. gummiferum* (Grass + *E.g*), (*2*) grass + *M. pubescens* (Grass + *M.p*) and (*3*) grass + *E. dysenterica* (Grass + *E.d*). Different letters indicate significant differences among treatment means, $p < 0.05$. *Arrows* ↑ indicate treatments with N addition

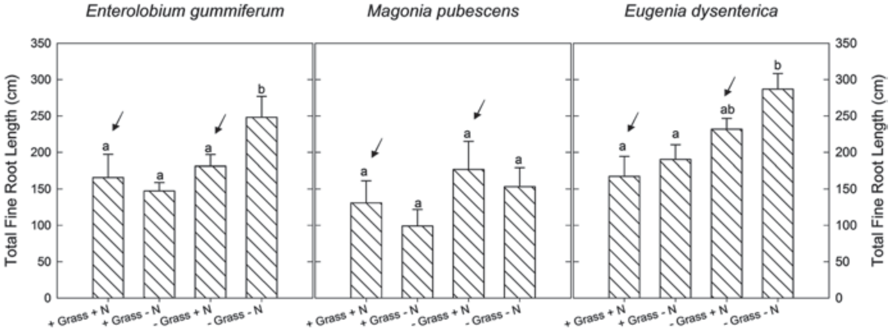

Fig. 22.3 Mean of total length of roots (cm) in *E. gummiferum*, *M. pubescens* and *E. dysenterica* growing in monoculture (−Grass) and in the presence of grass (+Grass, *E. inflexa*), without (−N) and with (+N) fertilization. Different letters indicate significant differences between treatment means, $p < 0.05$. *Arrows* ↑ indicate treatments with N addition

tive effects of interspecific competition, especially in the juvenile woody plants, increasing root biomass to levels similar to those found in the monocultures.

The effect of interspecific competition with the grass (*E. inflexa*) was even more obvious in the root morphology of the saplings, which were on average 12 and 28 % shorter in the presence of the grass without N addition (Grass − N) compared with the monocultures of *E. gummiferum* and *M. pubescens*, respectively. On the other hand, roots of *E. dysenterica* were about 14 % shorter in the treatment Grass + N (Fig. 22.3). In general, the addition of N counterbalanced or reduced the effect of competition (Fig. 22.3).

Under interspecific competition, the total root length and total fine root length diminished in two of the woody species and in the grass. *E. dysenterica* and *E. gummiferum* had higher total length of fine roots (up to 0.5 mm diameter) in the absence

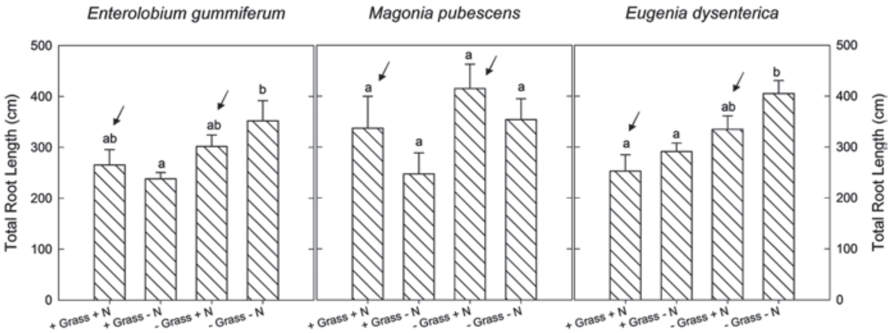

Fig. 22.4 Mean of total length of fine roots (up to 0.5 mm in diameter) in the three woody species growing in monoculture (−Grass) and in the presence of grass (+Grass), without (−N) and with (+N) fertilization. Different letters indicate significant differences between treatment means, $p<0.05$. *Arrows* ↑ indicate treatments with N addition

of the grass and without N addition (−Grass −N) (Fig. 22.4). *M. pubescens* presented the highest total length of fine roots in −Grass +N, without significant differences between the other treatments (Fig. 22.4). Root biomass was also reduced but only in one of these woody species.

22.4 Conclusion

The results provide an indication that competition between saplings of woody plants and grasses could be an important factor driving plant allometry and morphology during the first stages of development in Cerrado environments.

Our results also suggest that the responsiveness of plants to N deposition, as observed for other atmospheric nutrients or pollutants (Kozovits et al. 2005) depends in part on the type of competition (intra- or interspecific) occurring, and that this needs to be take into account in models of vegetation dynamics in response to nutrient deposition.

The enhancement of N availability might, in some cases, minimize the effects of competition, increasing the potential competitiveness of some woody species due to changes in total fine root length. The consequences of such changes in the competitive ability of plants in a long term, however, still have to be evaluated.

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