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A N   I N T E R N A T I O N A L   J O U R N A L

Allelopathic Evidence in *Brachiaria decumbens* and its Potential to Invade the Brazilian Cerrados

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ABSTRACT

The aim of this study was to look for evidence of allelochemicals in B. decumbens, *in parts of the plant from where they could easily be released to the environment. The germination inhibition of* Phalaris canariensis, Lactuca sativa *(standard species) and* Melinis minutiflora, *another invasive African grass, was tested using* B. decumbens *germinating seeds and aqueous leachates of the roots, green and senescent leaves, at 5, 10 and 20% w/v. Both the germinating seeds and the aqueous leachates of* B. decumbens *reduced the germination of the species tested; the effectiveness of the aqueous leachates increased according to concentration. Apparently, the competitive advantage of* B. decumbens *in the cerrados could be amplified via allelopathy.*

Keywords: allelopathy, cerrado, biological invasion, *Brachiaria decumbens*, *Melinis minutiflora*

INTRODUCTION

Biological invasion has been recognized world-wide as one of the worst environmental problems that lead to biodiversity loss (Vitousek *et al*., 1997; Wilcove *et al*., 1998; Pivello *et al*., 1999a; Mack *et al*., 2001). Invasive plant species combine a set of characteristics that enable them to outcompete the native species and dominate the invaded ecosystems. Some of these attributes are: vegetative and sexual reproduction, high productivity and high growth rates due to efficient photosynthetic processes and the effective use of nutrients, large production of easily dispersed seeds with high germination rates, short life cycles, and allelopathy (D'Antonio and Vitousek, 1992; Cronk and Fuller, 1995; Rejmánek and Richardson, 1996; Williamson, 1996; Kolar and

Lodge, 2001). Allelopathy, simply defined as "the release of phytotoxins by plants" (Bais *et al.*, 2003) can enhance the competitive success of the plant invaders, since the release of these phytotoxins in the environment may affect the growth and life processes of other community species (Whittaker and Feeney, 1971; Rice, 1984; Ridenour and Callaway, 2001; Callaway, 2002).

The Brazilian cerrado is recognized as the richest savanna in the world concerning plant species, and it integrates the list of global hot spots (Myers *et al*., 2000; Mittermeier *et al*., 2004). About 3,000 to 7,000 vascular plant species have been estimated for the cerrado *sensu lato* (following Coutinho´s [1978] classification) (Castro *et al*., 1999) and more than 6,400 vascular species have been registered for the cerrado region (Mendonça *et al*., 1998), which includes more than 20

physiognomies of savanna, forest, and grassland (Ribeiro and Walter, 1998). However, the great biodiversity of the cerrado biome is being severely threatened by a number of invasive exotic species, namely the African grasses *Brachiaria* spp., *Melinis minutiflora* Beauv., *Andropogon gayanus* Kunth, *Panicum maximum* Jacq., *Hyparrhenia rufa* (Nees) Stapf., once brought to the country as cattle forage. These grasses have spread in such a magnitude that they occur in virtually every cerrado fragment, outcompeting native herbs (Klink, 1996a; 1996b; Pivello *et al.*, 1999a; 1999b).

The high dominance of *Brachiaria* grasses over cerrado native herbs has recently raised investigations on the presence of phytotoxins in some species. In cerrados, *B. decumbens* (Nees) Stapf. has advanced massively throughout the native vegetation and formed monospecific patches with no other species growing below or close to it. *In situ* studies in São Paulo State cerrado areas have shown that even *M. minutiflora*, another East-African grass that invaded the cerrado, could have been displaced by *B. decumbens* (Pivello *et al.*, 1999a; 1999b), revealing a high competitive advantage of the latter species.

The present study aimed at looking for evidence of allelopathy in *Brachiaria decumbens* through bioassays, and exploring parts of the plant from where the supposed allelopathic substances could be easily released to the environment: seeds, senescent and green leaves, and roots. The inhibition of seed germination of *Lactuca sativa* L. cv Grand Rapids (Asteraceae) – a standard species for allelopathic tests –, *Phalaris canariensis* L. (Poaceae) – a (locally) non-invasive cultivated alien grass –, and of *Melinis minutiflora* Beauv. (Poaceae) – another grass invasive of cerrado – was tested.

MATERIALS AND METHODS

Plant material

Brachiaria decumbens Stapf (Poaceae) is native to East Africa and was introduced in Brazil in the 1950´s thanks to its high palatability to cattle, productivity, and resistance (Kissmann, 1997).

The cultivar Basilisk, introduced in São Paulo State, exhibits perennial and vigorous plants, with rigid erect leaves that form tussocks about 1 m high. It adapted very well to the cerrado soils and climate and became a very infesting species.

Melinis minutiflora Beauv. (Poaceae) is also native to East Africa. It was probably accidentally introduced in Brazil in the XIX century (Parsons, 1972; Filgueiras, 1990) and lately became a cattle fodder species. It is also perennial and erect, and forms 0.4 to 1 m high tussocks (Lorenzi, 1991) but not as dense as those of *B. decumbens*. *Melinis minutiflora* was chosen for testing against *B. decumbens* because it also showed a great competitive ability over cerrado herbaceous species and together with *B. decumbens*, it represented one of the most threatening invasive plants in the bioma (Pivello *et al.*, 1999a; 1999b).

Lactuca sativa L. cv. Grand Rapids (Asteraceae) is a standard species used in the tests of germination and allelopathy due to its high responsiveness and rapid germination (Ferreira and Aquila, 2000).

Phalaris canariensis L. (Poaceae) is a grass species not usually present in the cerrados but considered as an invader elsewhere in the world (ISI/TNC, 2005). Here, it was used as a Poaceae reference due to its high germination rates and availability.

The seeds of *B. decumbens*, *P. canariensis* and *L. sativa* were commercially acquired, whereas *M. minutiflora* seeds were field collected (July 2004).

Plant extracts

B. decumbens was cultivated in 8-l plastic pots with commercial garden soil and maintained in a greenhouse at room temperature (around 28ºC), 50% relative humidity, and natural light intensity reaching 1000 µmol maximum. Three months after the seeding, green leaves and roots were collected to make the extracts used in the tests. Senescent leaves were collected (September 2004) in the Cerrado Pé-de-Gigante Reserve (Vassununga State Park, SP).

Aqueous leachates of *B. decumbens* green leaves, senescent leaves and roots were prepared using 12.5, 25 and 50 g of the fresh material in 250 ml of distilled water. The plant material was fitted into Erlenmeyer tubes and then shaken for 12 h. The extracts were double filtered, resulting in 5, 10 and 20% w/v solutions, stored at 7º C.

Tests

The effects of the extracts and germinating seeds were tested adopting a full randomized design with six repetitions for each treatment and control groups. The seeds of *L. sativa* were allowed to germinate for three days while *P. canariensis* and *M. minutiflora* were allowed 10 days (following Brasil, 1992). To test for the allelopathic effects of *B. decumbens* germinating seeds, 30 of these and 30 seeds of the test species (*M. minutiflora*, *L. sativa* and *P. canariensis*) were put in Petri dishes (diameter = 11 cm) with moistened filter paper and incubated in germination chambers at 26º C, with 12 h light/darkness cycle. All the seeds had been previously sterilized with 1% sodium hypochlorite for 30 min and rinsed with distilled water (Yamamoto *et al.*, 1999; Higashinakasu *et al.*, 2004). Petri dishes and filter paper were sterilized in boiling water for 30 min. Germinated seeds were considered those with root equal or bigger than 1 cm (Copeland, 1976). The significance of the effects of *B. decubens* germinating seeds on other species was tested using a Mann-Whitney U test (Siegel and Castellan-Jr, 1988).

The allelopathic effect of the aqueous leachates of *B. decumbens* green leaves, senescent leaves and roots was also tested by placing 30 seeds of *M. minutiflora*, *L. sativa* and *P. canariensis* in Petri dishes with filter paper moistened with 2 ml of the aqueous extracts at 5, 10 and 20% (w/v). The control dishes were moistened with distilled water. The Petri dishes were then incubated in germination chambers at the same conditions as in the previous test. The percentages of germinated seeds in each Petri dish were angle-transformed prior to statistical treatment. The results of the tests using the aqueous leachates were submitted to a General Linear Model Analysis of Variance (GLM ANOVA). Significant effects were submitted to the *post hoc* pairwise tests of Tukey and Dunnet (Sokal and Rohlf, 2000).

RESULTS

In the presence of *B. decumbens* seeds, the germination of *L. sativa*, *P. canariensis* and *M. minutiflora* seeds decreased from 29.6 ± 0.51, 29.0 ± 1.26 and 29.6 ± 0.51 to 27.6 ± 1.86, 25.8 ± 4.26 and 22.3 ± 5.16, respectively. Although there was a general decrease in the germination, results were only significant for *M. minutiflora* ($p < 0.01$) (mean reduction = 23%). An overall increase of the standard deviation dispersion was another noticeable effect (Fig. 1).
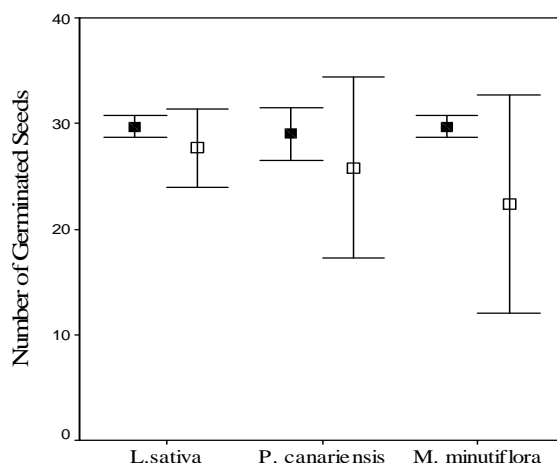

Figure1 - Mean (squares) and standard deviation (lines) from control (black squares) and experimental (empty squares) groups of *Lactuca sativa* (Asteraceae), *Phalaris canariensis* (Poaceae) and *Melinis minutiflora* (Poaceae) germinated seeds in the presence of *Brachiaria decumbens* (Poaceae) seeds.

The number of germinated seeds of the standard species (*L. sativa* and *P. canariensis*) was reduced when exposed to the aqueous leachates of *B. decumbens* organs (green leaves, roots and senescent leaves) at different concentrations (Table 1). The inhibitory response to the aqueous

leachates of *B. decumbens* on seed germination was more pronounced in *P. canariensis* (Table 1). However, the effects of the leachates at different concentrations were only significant against water alone (concentration 0% *versus* other concentrations) (Tables 1, 2) indicating that the effects were not proportional to the leachate concentration. Differential effects could not be attributed to different plant organs or to different leachate concentrations. The germination of *M. minutiflora* and *L. sativa* seeds was also significantly inhibited by the aqueous leachates of *B. decumbens* green leaves, roots and senescent leaves but only when comparing the results of distilled water and all the leachates (no proportional effect of the leachate concentration was observed) (Tables 1, 2).

Table 1 - Number of *Lactuca sativa* (Asteraceae), *Phalaris canariensis* (Poaceae) and *Melinis minutiflora* (Poaceae) seeds germinated when in contact with the aqueous leachates of *Brachiaria decumbens* (Poaceae) green leaves, senescent leaves and roots, at 5, 10 and 20% w/v (mean of six repetitions ± standard deviation).

	Extract concentration			
	0%	**5%**	**10%**	**20%**
Lactuca sativa				
green leaves	29.6 ± 0.21	28.6 ± 1.21	28.5 ± 1.68	28.6 ± 1.21
roots	29.6 ± 0.21	28.3 ± 0.81	26.5 ± 2.25	28.6 ± 1.21
senescent	29.6 ± 0.21	27.6 ± 0.51	28.6 ± 1.03	28.1 ± 1.47
Phalaris canariensis				
green	29.0 ± 1.26	25.0 ± 4.04	24.0 ± 4.28	19.3 ± 1.86
roots	29.0 ± 1.26	21.6 ± 4.50	22.0 ± 4.93	21.8 ± 4.32
senescent	29.0 ± 1.26	21.8 ± 7.05	20.0 ± 7.20	17.0 ± 2.09
Melinis minutiflora				
green leaves	29.3 ± 0.81	25.5 ± 0.83	27.6 ± 2.16	27.0 ± 2.28
roots	29.3 ± 0.81	25.8 ± 1.94	25.1 ± 2.63	25.5 ± 2.88
senescent	29.3 ± 0.81	27.8 ± 1.32	24.5 ± 2.42	25.3 ± 1.5

Table 2 - Results from GLM ANOVA considering the effects of aqueous leachates of *Brachiaria decumbens* (Poaceae) green leaves, senescent leaves and roots at different concentrations (5, 10 and 20% w/v) on the germination of *Lactuca sativa* (Asteraceae), *Phalaris canariensis* (Poaceae) and *Melinis minutiflora* (Poaceae), as well as the effects of the interactions among these factors.

Factor	*L.sativa*		*P. canariensis*		*M.minutiflora*	
	F	**p**	**F**	**p**	**F**	**p**
Organ	1.583	0.214	1.060	0.353	0.808	0.451
Leachate concentration	9.098	0.000	23.216	0.000	16.782	0.000
Organ X Leachate concentration	1.328	0.259	0.607	0.724	1.843	0.106

DISCUSSION

The results obtained here indicate possible allelopathic effects of *B. decumbens* on other species. These effects may occur at different stages of the *B. decumbens* life cycle and may come from different plant parts. During the germination stage, *B. decumbens* seeds were able to inhibit the germination of *L sativa*, *P. canariensis*, and especially of *M. minutiflora*. Plant-to-plant interactions at the germination stage through allelopathic inhibition of root and shoot growth have been reported by Higashinakasu et al. (2004) in seven crop and weed species, and by Laterra and Bazzalo (1999) between two invasive species of the pampa grasslands (Argentina).

Brachiaria decumbens allelopathic potential may remain throughout its lifetime including senescence, as the roots, green leaves and senescent leaves also showed allelopathic effects. Maciel et al. (2003) tested for allelopathic effects of *B. decumbens* dry leaves on the initial development of two crop legumes under agriculture conditions and obtained positive results for one of them. Indejit and Duke (2003) highlighted the advantage of the plants able to release phytochemicals from dead tissues, as their incorporation to the soil could be accelerated by leaching, thus facilitating their effects in the field.

Root exudates can be synthesized by plants and released to the soil by the live roots (Rice, 1984) and have been reported as an efficient strategy used by some *Centaurea* species (Bais *et al.*, 2003, Vivanco *et al.*, 2004) and *Echinochloa crus-galli* (Yamamoto *et al.*, 1999) – plants recognized as very aggressive invaders in North America.

Testing for the allelopathic inhibition of *Brachiaria* species on legumes, Almeida et al. (1997) and Fagioli et al. (1997) obtained positive results using the extracts of compressed green leaves and roots of *B.humidicola*, *B. decumbens* and *B. brizantha*. The greatest effects were revealed by *B. decumbens*. However, in the compressed material the cells are smashed and all the substances inside them are released. Therefore, this procedure is far from representing the field conditions. Alternatively, aqueous leachates can represent conditions closer to the natural ones.

In the present study, the inhibition effects were stronger over the grasses (Poaceae) *P. canariensis* and *M. minutiflora*, especially on the latter, compared to *L. sativa* (Asteraceae). A number of Poaceae family species have been pointed out as carrying allelopathic activity. Four main groups of phytotoxic compounds have been identified in Poaceae – phenolic acids, hydroxamic acids, alkalois, and quinones – which can be found in all parts of the plants, from pollen to root exudates (Steinsiek, *et al.*, 1982; Schumacher *et al.*, 1983; Anaya *et al.*, 1992; Einhellig and Souza, 1992; Hoffman *et al.*, 1996; Alsaadawi *et al.*, 1998; Kato-Noguchi and Ino, 2001; Sanchez-Moreiras, et al. 2004), and confer them a great advantage over other species.

Although the results here obtained came from a laboratory essay, they indicate the capacity of *B. decumbens* to release allelopathic substances to the environment. As in natural conditions, where a great number of interactions with the physical environment, as well as with other organisms, can enhance or restrain allelopathic effects, field experiments must be carried out to test the effectiveness of such allelopathic potential under natural conditions (Inderjit and Callaway, 2003). However, the great success of *B. decumbens* on invading cerrados could in part be due to allelopathy, as suggested in other parts of the world by authors who related allelopathy to biological invasions (Hiero and Callaway, 2003; Vivanco *et al,*. 2004; Ridenour and Callaway, 2001; Vaughn and Berhow, 1999).

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RESUMO

Invasão biológica é uma das maiores causas atuais da perda de biodiversidade. Várias espécies que se tornam invasoras produzem substâncias fitotóxicas que aumentam sua capacidade competitiva; assim, a alelopatia é uma estratégia capaz de potencializar o sucesso de invasão. *Brachiaria decumbens*, uma gramínea africana, invadiu os cerrados brasileiros e representa, atualmente, uma séria ameaça à biota regional. Neste ensaio, verificamos a presença de aleloquímicos em partes de *B. decumbens* das quais poderiam ser facilmente liberados para o ambiente. Testamos a inibição da germinação de *Phalaris canariensis*, *Lactuca sativa* (espécies-padrão) e *Melinis minutiflora* (outra gramínea africana invasora) usando sementes de *B. decumbens* e soluções aquosas lixiviadas de suas raízes, folhas verdes e folhas senescentes, a 5, 10 e 20% de peso do material por volume de água. Tanto as sementes como as soluções lixiviadas de *B. decumbens* reduziram a germinação das outras espécies; a eficiência dos lixiviados aumentou de acordo com a concentração da solução.

Acreditamos que a grande vantagem competitiva de *B. decumbens* no cerrado possa ser amplificada pela alelopatia.

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