The invasive grass, *Melinis minutiflora*, inhibits tree regeneration in a Neotropical savanna

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Abstract Exotic grasses are becoming increasingly abundant in Neotropical savannas, with *Melinis minutiflora* Beauv. being particularly invasive. To better understand the consequences for the native flora, we performed a field study to test the effect of this species on the establishment, survival and growth of seedlings of seven tree species native to the savannas and forests of the Cerrado region of Brazil. Seeds of the tree species were sown in 40 study plots, of which 20 were sites dominated by *M. minutiflora*, and 20 were dominated by native grasses. The exotic grass had no discernable effect on initial seedling emergence, as defined by the number of seedlings present at the end of the first growing season. Subsequent seedling survival in plots dominated by *M. minutiflora* was less than half that of plots dominated by native species. Consequently, at the end of the third growing season, invaded plots had only 44% as many seedlings as plots with native grasses. Above-ground grass biomass of invaded plots was more than twice that of uninvaded plots, while seedling survival was negatively correlated with grass biomass, suggesting that competition for light may explain the low seedling survival where *M. minutiflora* is dominant. Soils of invaded plots had higher mean Ca, Mg and Zn, but these variables did not account for the higher grass biomass or the lower seedling survival in invaded plots. The results indicate that this exotic grass is having substantial effects on the dynamics of the tree community, with likely consequences for ecosystem structure and function.

Key words: alien, Cerrado, competition, exotic species, invasive species, savanna.

INTRODUCTION

Grasses of African origin are planted widely throughout Neotropical savannas to increase productivity for cattle grazing. Several of these species are invasive, and are spreading within conservation areas (Pivello *et al.* 1999a), raising considerable concern regarding consequences for native species and ecosystem processes (Williams & Baruch 2000). Molasses grass (*Melinis minutiflora* Beauv.) is one particularly problematic species within the Cerrado region of central Brazil. Although it is no longer commonly planted as a pasture grass in favour of other, more productive, exotic grasses (Botrel *et al.* 1999), it is already widely distributed throughout the Cerrado and is abundant in many reserves in the region. In interviews with reserve managers and scientists in the Cerrado, this species ranked as the single greatest threat to nature reserves in the region (Pivello *et al.* 1999a).

Although much remains to be known about the impact of *M. minutiflora* on biodiversity, vegetation structure and ecosystem function in Neotropical savannas, available data indicate that impacts could be substantial. *Melinis minutiflora* commonly forms monodominant stands and produces higher biomass than native grasses (Hoffmann *et al.* 2004a), resulting in a sharp decline in herbaceous species diversity (Berardi 1994; Pivello *et al.* 1999b). The high biomass results in increased fire intensities (Mistry & Berardi 2005) which should result in higher rates of tree mortality and topkill (i.e. complete death of aerial biomass), as has been shown for tropical forests of Hawaii (D'Antonio *et al.* 2000), where this species also is invasive.

Even in the absence of fire, *M. minutiflora* may limit native tree regeneration. Previous studies have demonstrated that removal or clipping of exotic tropical grasses can increase establishment, survival and growth of tree seedlings (Morosini & Klink 1997; Holl 1998; Holl *et al.* 2000; Zimmerman *et al.* 2000; Griscom *et al.* 2005; Hooper *et al.* 2005; Denslow *et al.* 2006). However, these responses are not unique to exotic species, as removal of native grasses has similar effects (De Steven 1991; Van Auken & Bush 1997; Davis *et al.* 1999; Williams *et al.* 2005; Sharam *et al.* 2006; but see Brown & Archer 1999). Therefore, in savanna environments, it is not clear whether the displacement of native grasses by exotic grasses will have a large net effect on tree regeneration.

doi:10.1111/j.1442-9993.2007.01787.x

In the present study we performed a field experiment to test the effect of *M. minutiflora* on establishment, growth and survival of seven native tree species.

METHODS

The study was performed at the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE) and the adjacent Fazenda Água Limpa, a research station of the University of Brasília. These reserves are located near Brasília in the Federal District, Brazil at an elevation of approximately 1100 m. Mean annual rainfall at the meteorological station on the IBGE reserve was 1426 mm for 1993–2002, with a distinct dry season from May to September and mean annual temperature of 22.5°C.

Seeds of seven tree species were collected at the study site during the months of September to November of 2003. Five of the species are common in savanna environments, while the other two species are typical of adjacent gallery (riverine) forests (Table 1).

Forty plots (1 m × 2 m) were delimited in savanna sites with no woody cover directly overhead and with no adult individuals of any of the study species within close proximity. Twenty of these plots had native ground cover, hereafter referred to as native plots, while 20 were dominated by *M. minutiflora*, referred to as invaded plots. As is typical, *M. minutiflora* tended to form a dense monodominant canopy approximately 1 m tall, often with considerable accumulation of litter on the soil surface. In contrast, the native plots tended to have more open and shorter, mixed-species canopies, with relatively little litter accumulation. The plots were distributed widely across the 1300 ha IBGE reserve and part of Fazenda Água Limpa immediately adjacent to IBGE. Where possible, these plots were grouped in pairs of one invaded plot and one nearby native plot.

Each plot was divided into eight contiguous 50 × 50 cm subplots. One subplot was unused, whereas each of the remaining seven was sown with seeds of one study species on 18 December 2003. The arrangement of the species within the whole plot was the same for all plots. The number of seeds varied among species (Table 1), depending on availability. Seeds were sown in the subplots by scattering the seeds under the grass canopy without any disturbance to the litter or soil.

Censuses of seedling number and size were performed annually at the end of the growing season (May 2004, May 2005 and June 2006). Seedling height and basal diameter were measured with digital calipers. In September 2005, near the end of the dry season, an accidental fire at the study site burned nine of the native plots and nine of the invaded plots. In July 2006, we measured herbaceous biomass in the vicinity of each of the 22 unburned plots. We harvested the ground layer biomass within a 50 × 50 cm quadrat adjacent to the plot, dried the sample at 60°C, and weighed it on a digital balance.

In July 2006, a sample of the surface soil (0–10 cm) was collected near each plot. Soil pH was measured in 1:2.5 soil-water suspension and in 1 M KCl. Exchangeable Ca, Mg and Al were determined in soil extracts of 1 M KCl and exchangeable K and available P, Fe, Mn, Zn and Cu in Mehlich's extract of a diacid mixture of 0.05 M HCl and 0.0125 M H_2SO_4. The cations in soil extracts were determined by atomic absorption spectrophotometry and P by colourimetry (Allen 1989). Total N in soil was determined by Kjeldahl digestion and distillation. Soil organic carbon was determined by the method of Walkley and Black (Allen 1989).

Statistical analyses were performed with JMP 6.0.0 (SAS Institute, Cary, NC, USA). All tests were designed to ensure that plots, rather than individual seedlings, were treated as the sampling unit. We used a generalized linear model to test for effects of *M. minutiflora* and soil variables on seedling emergence, survival and final number. The analysis was performed with a binomial error structure with a logit link function. As the analyses often exhibited error overdispersion, an over-dispersion parameter was included in the model for all analyses.

To test for effects of *M. minutiflora* and soil variables on seedling height and diameter, a hierarchical analysis

Table 1. Tree species used in this experiment

Species	Family	Phenology	Habitat type	Number of seeds per plot
Aspidosperma subincanum Benth. ex Müll. Arg.	Apocynaceae	Deciduous	Forest	11
Brosimum gaudichaudii Trécul	Moraceae	Evergreen	Savanna	10
Kielmeyera coriacea (Spreng.) Mart.	Clusiaceae	Deciduous	Savanna	10
Piptadenia gonoacantha (Spreng.) J.F. Macbr.	Fabaceae, Mimosoideae	Evergreen	Forest	30
Qualea grandiflora Mart.	Vochysiaceae	Deciduous	Savanna	13
Qualea multiflora Mart.	Vochysiaceae	Deciduous	Savanna	25
Roupala montana Aubl.	Proteaceae	Evergreen	Savanna	30

of variance was performed, with seedlings nested within plots, and plots nested within treatments (i.e. native *vs.* invaded). To test for treatment effects, plot was designated as a random factor so that plot mean square was used as the error term, thereby ensuring that plots were treated as the experimental unit.

RESULTS

Seedling establishment and survival

Melinis minutiflora had no observable effect on seedling emergence, as defined by the number of seedlings present in May 2004, at the end of the first growing season (Fig. 1a). When considering all study species, an average of 27.7 seedlings per plot were present in invaded sites *versus* 32.0 seedlings per plot in native sites ($\chi^2 = 0.68$, $P = 0.41$). When tested for each species separately, there was no significant effect of *M. minutiflora* on the number of seedlings present at the end of the first growing season for any species ($\chi^2 < 3.41$, $P > 0.065$).

In contrast, *M. minutiflora* reduced subsequent seedling survival. From May 2004 to May 2006, *M. minutiflora* significantly reduced survival of five of the seven species (Fig. 1b). The two remaining species, *Qualea multiflora* and *Aspidosperma subicanum* tended to exhibit reduced survival in invaded plots, though this effect was not significant ($P = 0.09$ and $P = 0.11$, respectively). Over all species, the 2-year survival rates were 28.9% for invaded plots, *versus* 56.9% in native plots ($\chi^2 = 23.03$, $P < 0.0001$). The negative effect of *M. minutiflora* on seedling survival was significant both for 2004–2005 ($\chi^2 = 16.17$, $P < 0.0001$) and for 2005–2006 ($\chi^2 = 8.24$, $P = 0.004$).

The 2-year survival rates include the effect of an unplanned fire that occurred between the 2005 and 2006 censuses. Fire significantly reduced survival of two species. For *Roupala montana*, seedling survival from 2005 to 2006 was 12.3% ($n = 65$) in burned plots but 83.0% ($n = 71$) in unburned plots. For *Piptadenia gonoacantha*, the corresponding survival rates were 2.4% ($n = 85$) and 47.2% ($n = 36$). Equal numbers of native and invaded plots were burned, and there was no interaction between the effects of fire and *M. minutiflora* ($\chi^2 < 1.72$, $P > 0.19$), so the reduced survival in invaded plots cannot be explained by the occurrence of this fire.

At the end of the study, plots dominated by *M. minutiflora* had only 44% as many seedlings as plots with native grasses (8.0 *vs.* 18.3 seedlings per plot; $\chi^2 = 16.35$, $P < 0.0001$). When examined for each species, four of seven species had significantly fewer seedlings in plots dominated by *M. minutiflora* (Fig. 1c).
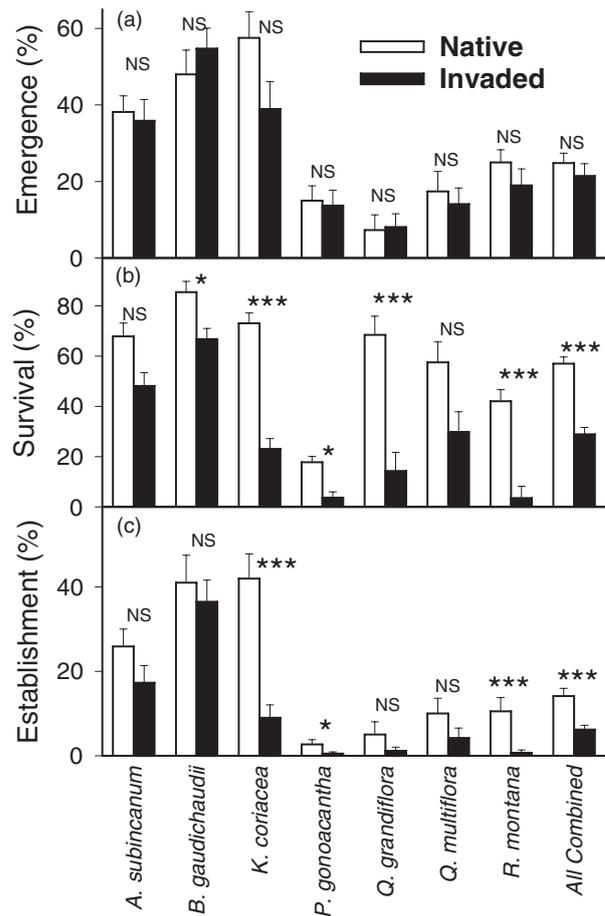

Fig. 1. Effect of the invasive grass, *Melinis minutiflora*, on seedling emergence, survival and establishment. (a) Emergence is defined as the number of seedlings present at the end of the first growing season per seed sown. (b) Survival rates are for the 2-year period beginning at the end of the first growing season. (c) Establishment is defined as the final number of seedlings present at the end of the experiment per seed sown. Symbols for statistical comparison of invaded *versus* native plots: *$P < 0.05$; **$P < 0.01$; ***$P < 0.005$; [NS]Not significant.

Seedling growth

In contrast to the results for survival, rates of height growth of several species were greater in invaded plots, relative to native plots. By the end of the second growing season, seedlings were taller in invaded plots relative to native plots for four of the seven species (Fig. 2). The subsequent year, these differences were significant among unburned plots only for *A. subincanum* and *P. gonoacantha*, as only 22 of the 40 plots remained unburned. Seedling basal diameter did not differ between invaded and native plots for any species either year (data not shown).
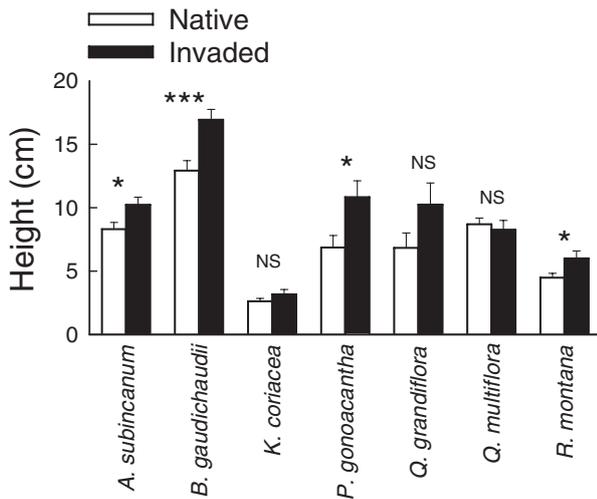
Fig. 2. Effect of the invasive grass *Melinis minutiflora* on seedling height at the end of the second growing season. Symbols for statistical comparisons defined as in Fig. 1.

Role of soil nutrients and ground layer biomass

There was no difference between invaded and native plots in P, C, N, Al, K, Mn, Cu, or pH in KCl ($P > 0.05$, Table 2), but plots with *M. minutiflora* had higher pH in H_2O ($t = 2.72$, $P = 0.01$) and higher availabilities of Ca, Mg and Zn ($t = 2.28$, $P < 0.03$, Table 2). Total grass biomass was 147% greater in plots dominated by *M. minutiflora* than in plots supporting native grasses (1275 g m^{-2} *vs.* 516 g m^{-2}, $t = 5.53$, $P < 0.0001$). Of the soil variables, only K, Mg, Mn and Al were significantly correlated with total grass biomass, but when these variables were taken into account, invaded plots continued to have significantly greater biomass than native plots (Fig. 3). Thus, the high biomass of plots invaded by *M. minutiflora* cannot be explained entirely by the higher availability of soil nutrients in these plots.

As grass biomass, soil pH, and available Ca, Mg and Zn differed significantly between invaded and uninvaded plots, we tested whether any of these differences contributed to the observed effects of *M. minutiflora* on seedling survival and growth. When included as a factor (together with fire and *M. minutiflora* effects) in the generalized linear model for seedling survival, none of these four soil variables had a significant effect on seedling survival of any of the study species. However, 2-year (2004–06) survival rates and final seedling number were negatively correlated with grass biomass (Fig. 4).

The soil variables generally were unable to explain the higher seedling growth rates in invaded plots that was observed for four species. When analyses of covariance were performed to test for effects of soil

variables, only five of the 91 possible tests (seven species by 13 soil variables) revealed a significant effect of a soil variable on seedling height. Of these significant tests, only one involved a species which was significantly taller in invaded plots (*Qualea grandiflora*) and a soil variable that differed between invaded and native plots (Zn; $F = 10.44$, $P = 0.048$).

DISCUSSION

Melinis minutiflora is a serious threat to plant biodiversity in the Brazilian Cerrado. The consequences of this exotic species for herbaceous communities have been previously shown (Berardi 1994; Pivello *et al.* 1999a), but here we found that it is also having strong negative effects on woody plant recruitment. Plots invaded by *M. minutiflora* had fewer than half the number of seedlings at the end of the experiment, relative to plots with native ground cover. This reduction is attributable to lower seedling survival in the second and third years of the experiment, rather than lower germination or emergence.

Seedlings of four tree species were taller in invaded plots than in native plots, seeming to contradict the trends for seedling survival. The taller seedlings in invaded plots cannot be explained by higher average nutrient availability in these plots, as seedling height was largely uncorrelated to soil nutrient availability. Possibly, the lower light availability under *M. minutiflora* may have resulted in etiolation or shifts in allocation. In a study of container-grown plants from this region, 15 of 18 woody plant species were significantly taller when grown under 74% shade than when grown in full sun, yet whole plant biomass did not differ consistently between treatments (reanalysed from Hoffmann & Franco 2003). In the current study, stem diameters were not significantly greater in invaded sites for any species, again suggesting that differences in allocation, rather than differences in relative growth rates, might explain the taller seedlings in invaded sites.

Low nutrient availability can strongly limit the success of *M. minutiflora* in native savanna (Barger *et al.* 2003). Nutrient requirements by this species may therefore explain why invaded plots had higher levels of pH, Ca, Mg and Zn than did native plots. Although there is little evidence that tree seedling growth and survival were directly affected by edaphic conditions, grass biomass was positively correlated with the availabilities of K, Mg, Mn and Al. Nevertheless, the higher mean nutrient status of invaded plots did not fully account for the higher grass biomass at these sites (Fig. 3), indicating that *M. minutiflora* inherently produces greater biomass than native grass communities over the range of soil conditions examined here. It is noteworthy that grass biomass was positively

Table 2. Mean soil chemical properties of the study plots

	Native plots	Invaded plots	t-value
pH in H_2O	4.67 (0.05)	4.91 (0.07)	2.72**
pH in 1 M KCl	4.28 (0.03)	4.33 (0.07)	0.57[NS]
C (%)	2.41 (0.08)	2.34 (0.11)	0.45[NS]
N (%)	0.198 (0.007)	0.175 (0.010)	1.81[NS]
P (mg kg^{-1})	0.500 (0.075)	0.679 (0.110)	1.34[NS]
K (cmol (+) kg^{-1})	0.134 (0.008)	0.139 (0.013)	0.32[NS]
Ca (cmol (+) kg^{-1})	0.215 (0.055)	0.489 (0.084)	2.73**
Mg (cmol (+) kg^{-1})	0.107 (0.014)	0.172 (0.020)	2.67*
Fe (mg kg^{-1})	64.50 (4.01)	55.02 (3.74)	1.73[NS]
Mn (mg kg^{-1})	15.13 (2.36)	15.47 (2.76)	0.09[NS]
Zn (mg kg^{-1})	1.051 (0.064)	1.349 (0.114)	2.28*
Cu (mg kg^{-1})	0.682 (0.030)	0.694 (0.050)	0.21[NS]
Al (cmol (+) kg^{-1})	0.923 (0.113)	0.743 (0.109)	1.15[NS]

Standard errors are in parentheses. Significance levels for t-test comparing native and invaded plots: *$P < 0.05$; **$P < 0.01$; NS, not significant.
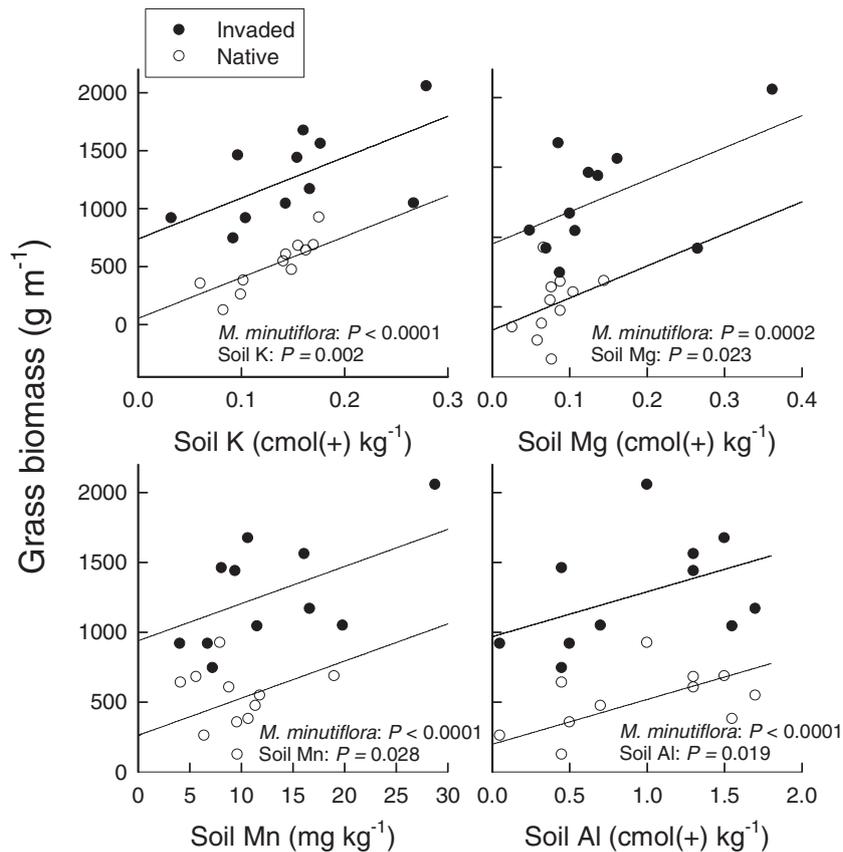

Fig. 3. Relationship between soil variables and grass biomass. Graphs are presented only for those soil variables that were significantly correlated with grass biomass. Plotted lines were derived from analysis of covariance, as slopes did not differ significantly between invaded and native plots in any of the analyses. As can be seen here, *Melinis minutiflora* produced significantly greater biomass than native grasses even when soil characteristics are taken into account.

correlated with both Al and Mn, two elements generally having toxicity effects on annual crops planted in unlimed Cerrado soils (Fageria & Baligar 2001). The positive correlation between grass biomass and these elements shows that toxicities of these elements are not limiting factors for either native or the exotic species.

The dense cover generated by *M. minutiflora* may largely be responsible for the reduced tree seedling
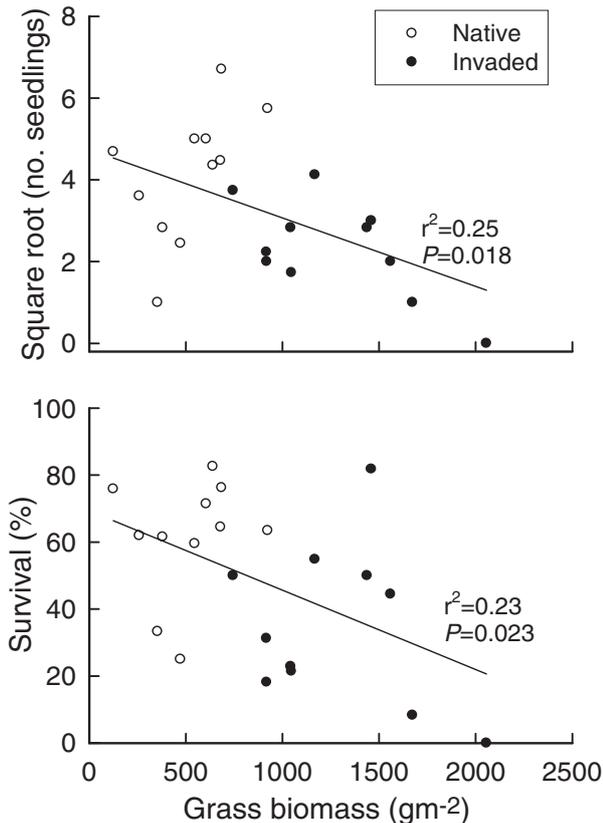
Fig. 4. Relationship between grass biomass and number of seedlings per plot at the end of the study in 2006 (top) and the 2-year survival rate (bottom). Seedling data were pooled across all species.

survival. Invaded plots had more than twice the grass biomass as native plots, and tree seedling survival was negatively correlated with grass biomass. This corroborates previous results demonstrating that low sapling densities in invaded sites were associated with higher grass leaf area index and biomass (Hoffmann *et al.* 2004a). Savanna tree species are generally intolerant of deep shade, as evidenced by low survival of seedlings (Hoffmann *et al.* 2004b) and absence of adults (Felfili & Junior 1992) in nearby forests, so low light availability may have limited the success of seedlings in invaded plots. Similarly, *P. gonoacantha,* the one forest tree species exhibiting a significant decline in survival in invaded plots, is considered a shade-intolerant pioneer (Carvalho 2003).

Alellopathy can also play an important role for the success of invasive species (Callaway & Ridenour 2004). Extracts of *M. minutiflora* include propionic acid, butyric acid and 1,8-cineole (Prates *et al.* 1998), all of which have been shown to reduce germination and/or seedling growth (Janovicek *et al.* 1997; Koitabashi *et al.* 1997; Chaves *et al.* 2001). Unfortu-

nately, our data are insufficient to determine the relative importance of competition and allelopathy for the effects observed here.

Understanding the mechanism by which *M. minutiflora* reduces seedling survival is necessary if we are to extend these results to tree population dynamics. Once a tree successfully overtops the herbaceous layer, it could still be affected by allelopathy, but would escape shading by *M. minutiflora*. Nevertheless, even if light availability were the primary factor limiting seedling survival in invaded sites, we cannot assume that the effect of *M. minutiflora* on tree seedlings will be short-lived. Tree seedling growth is extremely slow in the Cerrado (Hoffmann 2000; Franco 2002), so a decade or more may be required for seedlings to overtop *M. minutiflora* and avoid shading. The cumulative effect of many additional years of high mortality may be sufficient to effectively curtail tree recruitment in sites heavily invaded by *M. minutiflora*.

For saplings that do succeed in surpassing the height of *M. minutiflora*, fire may continue to constitute a barrier to tree success in invaded sites. The high biomass of *M. minutiflora* results in more intense fires (Mistry & Berardi 2005), which will result in higher rates of tree topkill. Although established savanna trees typically resprout following topkill, the loss of aerial stems has important consequences for vegetation structure and tree population dynamics. Under frequent burning and low tree growth rates typical of tropical savanna, repeated topkill maintains saplings in a diminutive state (Higgins *et al.* 2000; Hoffmann & Solbrig 2003). An increase in fire intensity resulting from the presence of *M. minutiflora* would aggravate this effect, resulting in lower tree cover.

Understanding the full consequences of *M. minutiflora* for Cerrado biodiversity will require longer-term monitoring of the entire plant community. But this may be complicated by ongoing changes in the intensity of competitive interactions. In a controlled study, the competitive effect of *M. minutiflora* on the growth of a native grass was enhanced by elevated CO_2 (Baruch & Jackson 2005).

Regardless of the mechanisms involved, there is little question that this and other exotic grasses pose a serious threat to conservation in the Cerrado. Over 40% of the Cerrado region has been transformed to pastures planted with exotic grasses while the remaining natural vegetation is quickly being converted to either exotic pasture or mechanized agriculture (Klink & Machado 2005). This rapid land-use change emphasizes the importance of protected areas for biodiversity conservation. Considering that many, if not all, of Cerrado parks and reserves already suffer from the effects of exotic grasses, there is an urgent need to develop management practices that can slow or reverse their spread.

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