



The role of topkill in the differential response of savanna woody species to fire

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Abstract

Understanding the impact of fire on the demography of savanna trees and shrubs is necessary for understanding human impacts in tropical savannas. In a replicated experiment, we studied the impact of fire and vegetation cover on survival and growth of two subshrubs (*Periandra mediterranea* and *Protium ovatum*), two shrubs (*Miconia albicans* and *Rourea induta*) and three trees (*Myrsine guianensis*, *Piptocarpha rotundifolia* and *Roupala montana*) of the Brazilian cerrado savannas. Burning increased complete mortality (i.e. death of the individual) of five of the seven species, but primarily among individuals with stem diameters <4 mm. Stem mortality (i.e. topkill) was much more prevalent, primarily affecting individuals with stem diameter <32 mm, though all species experienced some topkill in even the largest size classes. Fires of higher intensity (flame length >2 m) caused greater mortality and topkill than fires of lower intensity (flame length <2 m). Pre-burn vegetation density had little effect on survival or resprout size, but did affect subsequent growth rates. Four species had greater growth rates in open sites, whereas only one species had greater growth rates in dense sites. For the three tree species and one shrub, resprouting individuals did not reach the minimum reproductive size within 1 year of burning, while the other shrub and the two subshrubs were able to reach reproductive size during this time, indicating that growth form largely determines the population response to frequent burning. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Understanding the factors responsible for the great variation in woody plant density in tropical savanna has been a considerable challenge to understanding the dynamics of this biome. Perhaps the most common view today is that no single factor determines tree

density in savannas; rather, nutrient availability, water stress, herbivory and fire interact to determine woody plant cover (Frost et al., 1986). In the neotropical savannas, where there are few browsing mammals, it is arguably most important to understand the role of fire, since only this one is largely under human control and is the most likely to be responsible for temporal changes in woody plant density within the time frame of human observation.

Indeed, frequent fire is a serious environmental problem in many moist tropical savannas throughout

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the world. Fire intervals of 2–3 years are common in these regions (Trollope, 1984; Coutinho, 1990; Menaut et al., 1991; Russell-Smith et al., 1997), largely due to anthropogenic burning. Savanna tree communities exhibit a high degree of resilience to individual fires (Felfili et al., 2000), presumably due to the low mortality and rapid resprouting (Rutherford, 1981; Sato and Miranda, 1996; Trollope, 1996). However, even low rates of mortality may not be sufficient to guarantee persistence under frequent burning. Low rates of fire-induced tree mortality, compounded over multiple fires can cause considerable loss, while many of those individuals that survive burning are subjected to topkill (i.e. death of the aerial biomass).

Large individuals may resist topkill due to thick bark, but small individuals cannot (Rutherford, 1981; Gignoux et al., 1997), since bark thickness is largely dependent on stem diameter (Hedge et al., 1998). If burning is frequent, these small individuals may be unable to grow into larger size classes, remaining indefinitely in a reduced, often non-reproductive stage (Rebertus et al., 1993). Similarly, even some large mature individuals may be subjected to topkill (Williams et al., 1999), thus reverting to small size classes, with this reduction being effectively irreversible if fire is too frequent. These reduced individuals will remain in this state unless a sufficient fire-free interval occurs to attain sufficient size and bark thickness to resist topkill. Therefore, topkill and the rate of resprout may control changes in tree cover in moist tropical savannas (Bond and Midgley, 2000; Higgins et al., 2000).

The reduction in size due to topkill can greatly reduce sexual reproduction of savanna trees and shrubs because seed production is positively related to plant size (Hoffmann, 1998). If frequent fire maintains an individual at a size smaller than the minimum reproductive size, then sexual reproduction can be curtailed altogether (e.g. Van Wyk, 1971 cited in Rutherford, 1981). This, combined with even low rates of mortality would be sufficient to drive population decline in the absence of some mode of clonal propagation.

Due to topkill, under the short fire intervals typical today, reproductive size can probably be reached only with high growth rates or if sexual maturity is reached at a small size class. To be able to cope with these limitations, it is expected that frequent burning would select for species with thick bark, rapid regrowth, and

reproduction at small size. Savanna species appear to differ in the extent to which they invest in these various strategies. For example, among West African savanna trees, *Crossopteryx febrifuga* invests in greater fire resistance in the form of thicker bark, while *Piliostigma thonningii* invests in greater aboveground growth rates (Gignoux et al., 1997). Subshrubs may represent an alternative strategy, investing little in permanent aboveground structures and attaining reproductive maturity at a small stem size. Following burning, the minimum reproductive size is reached quickly by resprouting.

It is within this context that we compare the effects of fire on topkill and regrowth of seven cerrado savanna species ranging from subshrubs to trees. We also examine the effect of phenological state on regrowth of several species. Many cerrado species produce a new flush of leaves before the end of the dry season, so late dry-season burns occur when many species have invested a large amount of carbohydrate and nutrients in new leaves, reducing the amount available for resprouting (Glitzenstein et al., 1995; Drewa et al., 2002).

Another aspect of savanna ecology which has been largely unexamined is how tree growth and survival respond to the great spatial variability in tree density typical of tropical savannas, even though this may play an important role in determining the balance between trees and grasses (Menaut et al., 1990). In the cerrado, vegetation ranges from open grassland (campo limpo) to nearly closed canopy woodland (cerradão). Intermediate forms include campo sujo (open shrub savanna), cerrado *sensu stricto* (tree and shrub savanna). This variation may affect plant performance through competition or may reflect variations in edaphic factors which themselves are responsible for this variation in tree density. Here we test whether this variation in tree density is associated with growth and survival of the seven study species.

2. Methods

The seven study species range in stature from subshrub to tree: *Periandra mediterranea* Taub. (subshrub, Leguminosae), *Protium ovatum* Engl. (subshrub, Burseraceae), *Miconia albicans* Steud. (shrub, Melastomataceae), *Rourea induta* Planch.

(shrub, Connaraceae), *Myrsine guianensis* Aubl. (syn. *Rapanea guianensis*, tree, Myrsinaceae), *Piptocarpha rotundifolia* (Less.) Baker (tree, Compositae), *Roupala montana* Aubl. (tree, Proteaceae). All are evergreen species and are abundant at the study site, and at least the tree and shrubs are common throughout much of the cerrado (Ratter et al., 1996). As is typical of most or all cerrado woody plants, all of the study species resprout following fire. In parallel studies, fire reduced seed production of *Periandra*, *Miconia*, *Rourea*, *Myrsine*, and *Roupala*, while increased that of *Piptocarpha* (Hoffmann, 1998). *Miconia* and *Myrsine* appear capable of forming soil seed banks, but there is little evidence that fire stimulates germination. In fact, fire reduced seedling establishment of these species as well as for *Roupala* and *Periandra* (Hoffmann, 1996). *Roupala*, *Myrsine*, *Rourea*, *Piptocarpha*, and *Protium* are capable of clonal spread by producing root suckers at some distance from the original plant. For at least the first three of these species, fire enhances the production of these root suckers (Hoffmann, 1998).

This study was conducted near Brasilia, Brazil at 15°56'S and 47°53'W within the experimental area of a large fire project located at the ecological reserve of the Instituto Brasileiro de Geografia e Estatística (IBGE), and the adjacent Jardim Botânico de Brasília (JBB). Study plots were established in tracts subjected to one of two fire regimes—no burn (control) and biennial late season burn. Each of these fire regimes was replicated in six experimental tracts. In each of the two reserves (IBGE and JBB) one tract of each regime was established in campo sujo (open shrub savanna), cerrado *sensu stricto* (tree and shrub savanna) and cerrado (dense woodland). These tracts range from 4 to 10 ha, surrounded by a firebreak and had not been burned for at least 7 years prior to the first experimental burns studied here.

A 15 m × 25 m study plot was established in each of these 12 experimental tracts. Individuals of all seven study species were marked with a numbered aluminum tag and mapped to within 10 cm to ensure finding all individuals in subsequent censuses. Large individuals lying outside the permanent plot, but subjected to the same fire regime, were also included to increase the sample of individuals in the largest size classes, which were underrepresented in the plots.

Annually, during the dry season before the time of burning the plots, stem diameter was measured of all individuals of the study species. For individuals with height greater than 60 cm, stem diameter was measured 30 cm from the ground. For individuals less than 60 cm tall, stem diameter was measured at one-half the height of the plant. For individuals with stem diameter ≤20 mm, diameter was measured with digital calipers. For individuals with stem diameter >20 mm, stem diameter was measured with a diameter tape.

The six plots located in IBGE were established and first censused in 1992 and the six plots located in JBB were established and first censused in 1993, prior to the first burns in each of these reserves. An exception is the campo sujo control plot in IBGE, which was first censused in 1993. Censuses were performed during 1992–1995. The total number of plant-years of data were *Miconia* (3756), *Myrsine* (4821), *Periandra* (976), *Piptocarpha* (660), *Protium* (324), *Roupala* (2952), and *Rourea* (3653).

All burns occurred in late September or early October, corresponding to the end of the dry season. For each fire, observations were made to estimate flame length within the 15 m × 25 m plot or as near as possible, depending on the visibility of the plot from the firebreak. Maximum and minimum flame lengths within the vicinity of the plot were recorded, and the burns were subsequently categorized as low intensity (flame length <2 m) or high intensity (flame length >2 m). Additionally, in 1994, an uncontrolled fire spread through the experimental area, burning many of the plots. In JBB this fire burned the control plots in cerrado and cerrado *sensu stricto*, as well as the burn plots in campo sujo and cerrado *sensu stricto*. In IBGE, the fire burned the control plots in cerrado *sensu stricto* and cerrado. Details of the fire regimes are provided in Table 1.

Prior to several of the burns, the phenological state of a subset of the individuals was scored to quantify the degree of leaf expansion. Each of these individuals were assigned a score ranging from 0 (no bud expansion) to 5 (leaf expansion completed) on the day burning was performed. This was done for all species except *Miconia* and *Myrsine*, for which leaf production does not occur in discrete events, making it difficult to classify leaf expansion.

Bark thickness of 30 individuals each of *Rourea*, *Roupala*, *Piptocarpha*, and *Myrsine* was measured

Table 1
Burn schedule for the 12 study plots

Plot	Reserve	Vegetation type	Last burn prior to 1992	Experimental burns			
				1992	1993	1994	1995
1	IBGE	Campo sujo	1973	H		H	
2	IBGE	Campo sujo	1973				
3	IBGE	Cerrado <i>sensu stricto</i>	1973	L		H	
4	IBGE	Cerrado <i>sensu stricto</i>	1973			H	
5	IBGE	Cerradão	1973 ^a	L		H	
6	IBGE	Cerradão	1973 ^a			L	
7	JBB	Campo sujo	1989		H	L	
8	JBB	Campo sujo	1989				
9	JBB	Cerrado <i>sensu stricto</i>	1989		L	L	
10	JBB	Cerrado <i>sensu stricto</i>	1989			H	
11	JBB	Cerradão	1989 ^a		L		
12	JBB	Cerradão	1989 ^a			H	

Letters denote fire intensity (L: low intensity (flame length <2 m); H: high intensity (flame length >2 m)). Years without a letter indicate that the plot was not burned at that time. All burns were performed at the end of the dry season (September to October). Vegetation types are campo sujo (open shrub savanna), cerradão (woodland with nearly closed canopy) and cerrado *sensu stricto* ('typical' cerrado with intermediate tree density).

^a Due to lower flammability, areas of cerradão might not have burned when the other areas burned in previous years.

with a JIM-GEM bark gauge in an unburned plot. The remaining species have thin bark that cannot be measured easily with the gauge. The bark thickness was measured at 30 cm height at two points, and these two values were averaged. For species with ridged bark, thickness was measured at the ridges, rather the troughs between ridges.

We used logistic regression to test whether stem diameter, burning, vegetation density, and time since last burn affected mortality and to determine whether stem diameter and fire intensity affected topkill. A modified, four-parameter logistic equation was used to provide a more realistic fit to the mortality data: $mortality = C / (1 + \exp(A \log_{10} dia + B)) + D$, where A , B , C , and D are parameters. This model allows the curve to reach asymptotes other than 0 and 1, often permitting a much better fit than the traditional logistic regression equation. This is particularly relevant for large size classes where mortality sometimes approaches a non-zero value with increasing size. The equation was fit using the nonlinear regression module of SPSS 7.0 with a maximum likelihood loss function. The likelihood ratio test was used to compare this model with simpler models in which $C = 1$ and $D = 0$. When the more complex model did not significantly improve the model fit, the simpler model is reported.

To relate diameter increment to initial diameter, we used the computer program CurveExpert 1.2 to choose a nonlinear model that consistently produces a good fit for all species. This program fits a large number of nonlinear equations to the data, subsequently ranking the data according to r^2 -values. For the second year after burning, the logistic curve was found to produce a good fit for all species. For regrowth of topkilled individuals in the first year after burning, and for diameter increment in unburned plots, we found the exponential association function $I = a(1 - \exp(-b(\text{dia})))$ to produce the best fit, where I is diameter increment.

Upon determining which model was to be used, final curve-fitting and analyses were performed with the nonlinear regression module of SPSS 7.0 using least squares regression. To test for an effect of vegetation density, this model was compared to the more complex models in which the parameters a and/or b were allowed to differ between vegetation types. The sum of squares of a more complex model (SS_2) was compared to the sum of squares of the simpler model (SS_1), using the F -test performed on the value $F = (SS_2 - SS_1) / MS_{\text{error}}$ (Zar, 1999), where MS_{error} is the error mean square for the more complex model. If the more complex model produced a significantly better fit, this result is reported.

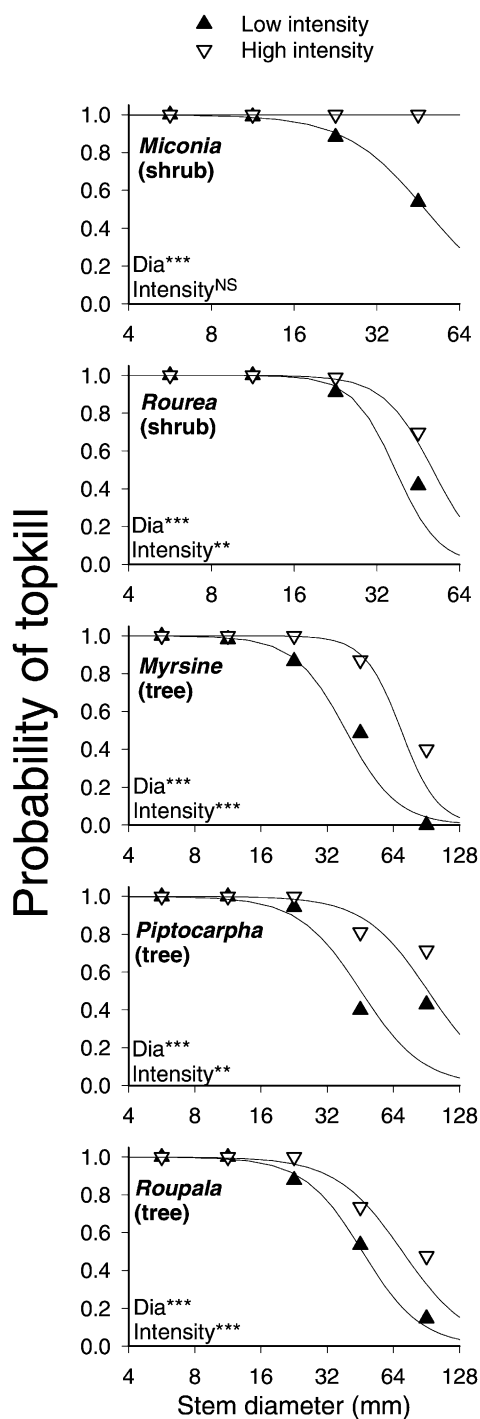


Fig. 1. Effect of fire intensity on topkill (stem mortality) of the five tree and shrub species. In every case except *Miconia*, high-intensity fires (flame length >2 m) caused significantly greater stem mortality than low-intensity fires (flame length <2 m) as determined by logistic

3. Results

3.1. Topkill

The two subshrub species, *Protium* and *Periandra*, experienced 100% topkill, regardless of stem diameter and fire intensity. For all the remaining species, topkill was 100% for small individuals and declined with stem diameter (Fig. 1). For *Rourea*, *Myrsine*, *Piptocarpha*, and *Roupala*, topkill was significantly greater in high-intensity burns (flame length >2 m) than low-intensity burns (flame length <2 m) (Fig. 1).

Bark thickness was strongly and positively correlated to stem diameter for the four species examined (Fig. 2) ($r^2 \geq 0.77$, $P < 0.001$). For each species, we used the logistic regression equations shown in Fig. 1 to calculate the diameter at which 50% topkill occurred, and used the regressions of Fig. 2 to estimate the corresponding bark thickness. In low-intensity fires, 50% stem survival occurred at smaller stem diameters and bark thicknesses than in high-intensity burns. For low-intensity burns, the stem diameter at which 50% of stems survived burning ranged from 37 to 46 mm among species, corresponding to bark thickness of 6–7 mm (Table 2). For high-intensity burns, the stem diameter at which 50% of stems survived burning ranged from 51 to 91 mm, with bark thickness of 9–13 mm (Table 2).

3.2. Mortality

There was a significant relationship between stem diameter and mortality for all species, with smaller individuals experiencing greater mortality (Fig. 3). Burning significantly increased mortality for all species except *Piptocarpha* and *Protium*, the species with the lowest sample sizes (Fig. 3). Relative to low-intensity burns, high-intensity burns caused a small but significant increase in mortality for *Protium* ($P=0.03$), *Miconia* ($P < 0.0001$), *Myrsine* ($P=0.03$),

regression. The symbols represent the observed fraction of individuals in a given size class that experienced stem mortality. The two subshrub species are not shown because all individuals experienced stem mortality regardless of fire intensity. The regression equations are provided in the Appendix A. Significance levels for effects of stem diameter and fire intensity: (NS) not significant; (**) $0.001 < P < 0.01$; (***) $P < 0.001$.

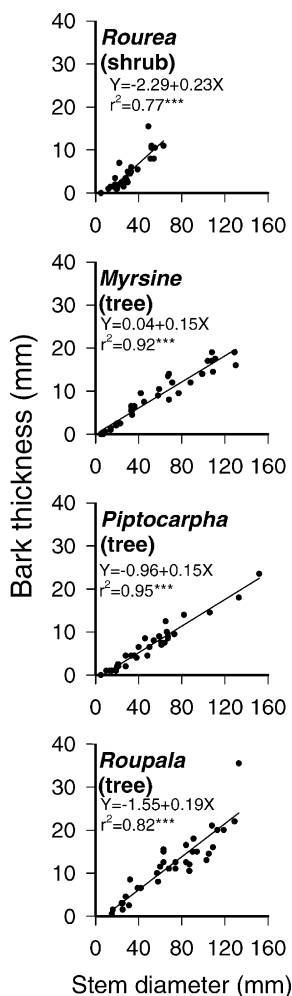


Fig. 2. Relationship between stem diameter and bark thickness for four of the study species. For all species there was a highly significant relationship between stem diameter and bark thickness ($P \ll 0.001$).

and *Roupala* ($P = 0.0007$), but not for *Periandra* ($P = 0.79$), *Piptocarpha* ($P = 0.10$) and *Rourea* ($P = 0.54$, data not shown). Vegetation density did not influence survival in burned plots, but in unburned plots *Myrsine* had significantly higher survival in dense plots relative to the other plots ($P = 0.004$).

3.3. Resprouting

For topkilled individuals there was a strong positive relationship between pre-burn stem diameter and stem

Table 2

Stem diameter and bark thickness at which 50% stems are topkilled

Species	Stem diameter (mm)		Bark thickness (mm)	
	Low intensity	High intensity	Low intensity	High intensity
<i>Rourea</i>	37	51	6.3	9.4
<i>Myrsine</i>	39	69	6.3	11.0
<i>Piptocarpha</i>	46	92	6.1	13.2
<i>Roupala</i>	46	70	7.3	12.0

The diameter at which 50% topkill occurred was determined from the logistic regression curves of Fig. 1, and the corresponding bark thickness was determined from the linear regressions of Fig. 2.

diameter of resprouts 1 year after burning, with the curve approaching a maximum resprout stem diameter (Fig. 4). Larger growth forms tended to have larger maximum resprout size; for the two subshrubs, maximum resprout diameters were 3–4 mm 1 year after fire, while for the trees, the maximum resprout diameters ranged from 8 to 15 mm. Maximum resprout diameters of the shrubs were intermediate, having values from 5 to 10 mm (Fig. 4).

Despite the smaller resprout sizes of the smaller growth forms, they had a greater capacity to regain reproductive size (Fig. 4). For both subshrubs, the maximum resprout diameter 1 year after burning was greater than the minimum reproductive size, while for the three tree species, maximum resprout diameter was only 20–37% of the minimum reproductive size. As for the shrubs, resprouts of *Miconia* were slightly smaller than reproductive size while those of *Rourea* were larger (Fig. 4). The minimum reproductive sizes used here were obtained from censuses described by Hoffmann (1998).

Very small individuals were likely to regain their pre-burn size within a year of burning, while very large individuals were likely to retain their pre-burn size by avoiding topkill (Fig. 5). There was a range of stem diameters, approximately 10–20 mm, for which few or no individuals were able to quickly regain their pre-burn size nor avoid topkill (Fig. 5).

Resprout size responded to vegetation density only for *Periandra* and *Roupala*. For *Roupala*, resprout diameter was 11% greater in the dense (cerradão) sites than in the more open sites ($P \ll 0.001$), while

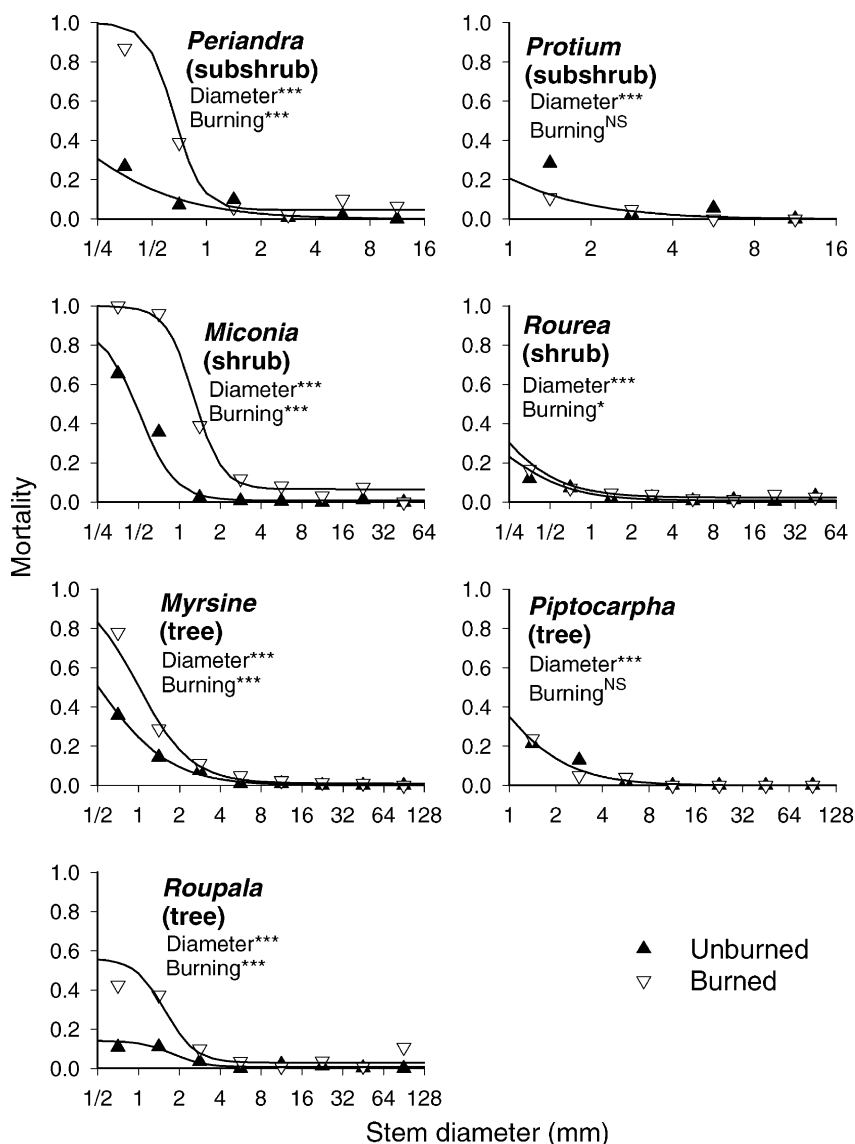


Fig. 3. Effect of burning on mortality. There was a significant decline in mortality with stem diameter for all species. All species except *Piptocarpha* and *Protium*, for which sample sizes were low, experienced greater mortality when burned. The symbols represent the observed fraction of individuals killed within a size class, and the curves represent the logistic regressions fit to the data.

resprout diameter for *Periandra* was 8% lower in dense sites ($P = 0.001$, data not shown).

Analysis of covariance was used to test if phenological state influenced resprout growth after controlling for pre-burn size. No species exhibited a significant relationship between phenological state at time of burning and resprout length (Table 3).

3.4. Growth

Mean diameter growth increased with stem diameter, approaching a maximum value for large stem diameters (Fig. 6). Mean diameter growth rates of unburned plants of the largest size classes ranged from <0.5 mm per year to nearly 4 mm per year.

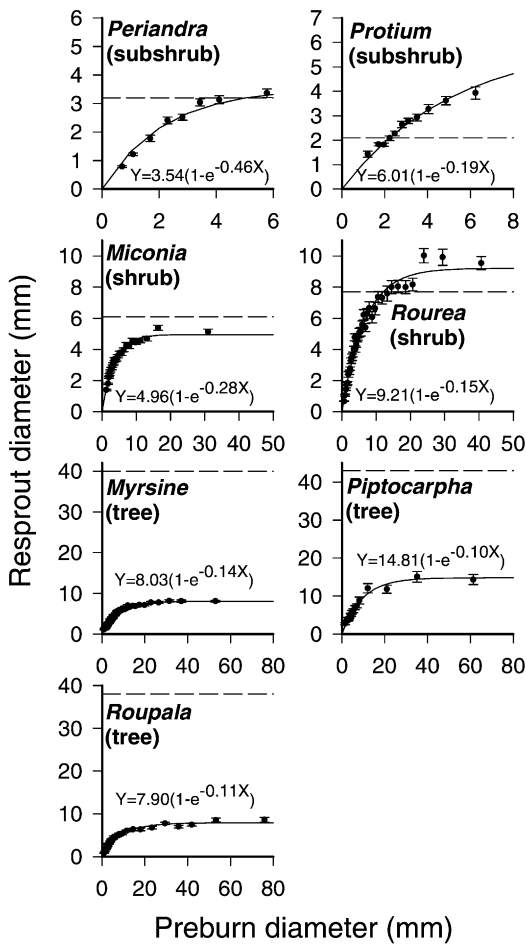


Fig. 4. Relationship between pre-burn stem diameter and post-burn stem diameter, 1 year after burn. The figure includes only those individuals that experienced topkill. The dashed horizontal lines indicate the minimum reproductive size for each species, obtained from reproduction censuses described by Hoffmann (1998). The symbols and error bars represent the observed mean and standard error for groups of individuals. For *Protium*, *Periandra* and *Piptocarpha*, 25 individuals were included in each mean; for the remaining species, 50 individuals were included.

Diameter growth of plants was strongly dependent upon time since last fire. Topkilled plants in the second year after burning exhibited higher growth rates than those not burned recently (Fig. 6). However, for those individuals that were not topkilled, growth did not differ significantly between unburned plants and plants in the second year after burning for *Miconia*, *Rourea*, *Piptocarpha*, and *Roupala*.

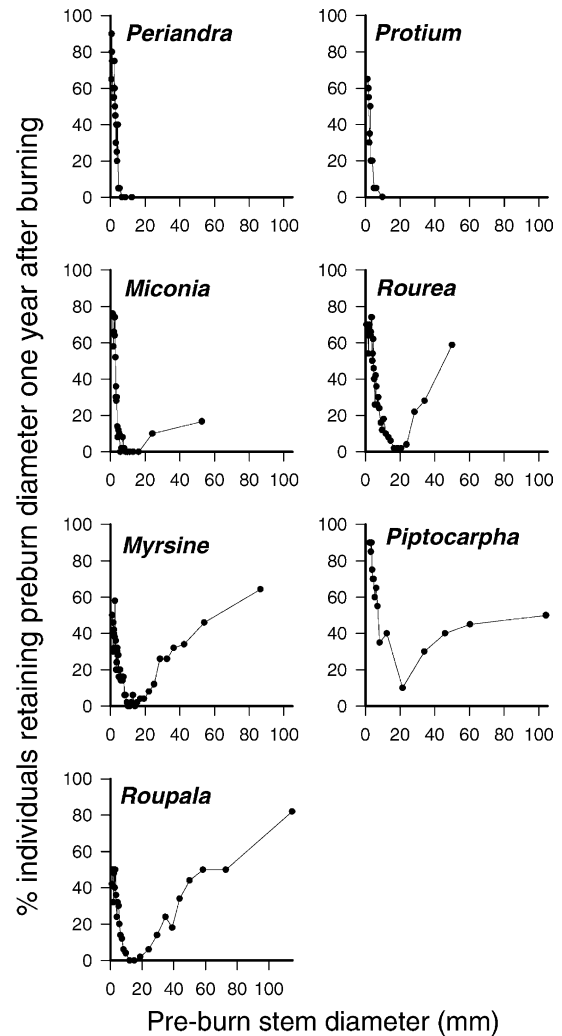


Fig. 5. The fraction of individuals for which stem diameter 1 year after burning was greater than or equal to the pre-burn stem diameter. Small-stemmed individuals were all topkilled, but 1 year after burning many had regained the pre-burn size. Many large-stemmed individuals retained their stem diameter by avoiding topkill, but those that were topkilled were unable to regain their pre-burn size. Individuals of intermediate size were neither able to avoid topkill nor regain their initial size within a year after burning. The symbols represent the observed mean for groups of individuals. For *Protium*, *Periandra* and *Piptocarpha*, 25 individuals were included in each mean; for the remaining species, 50 individuals were included.

For *Myrsine*, burned plants had lower growth than unburned plants of similar size (2.5 mm per year versus 3.7 mm per year; $P = 0.001$). Note that we did not quantify growth in the year that burning occurred, since consumption of the outer bark often

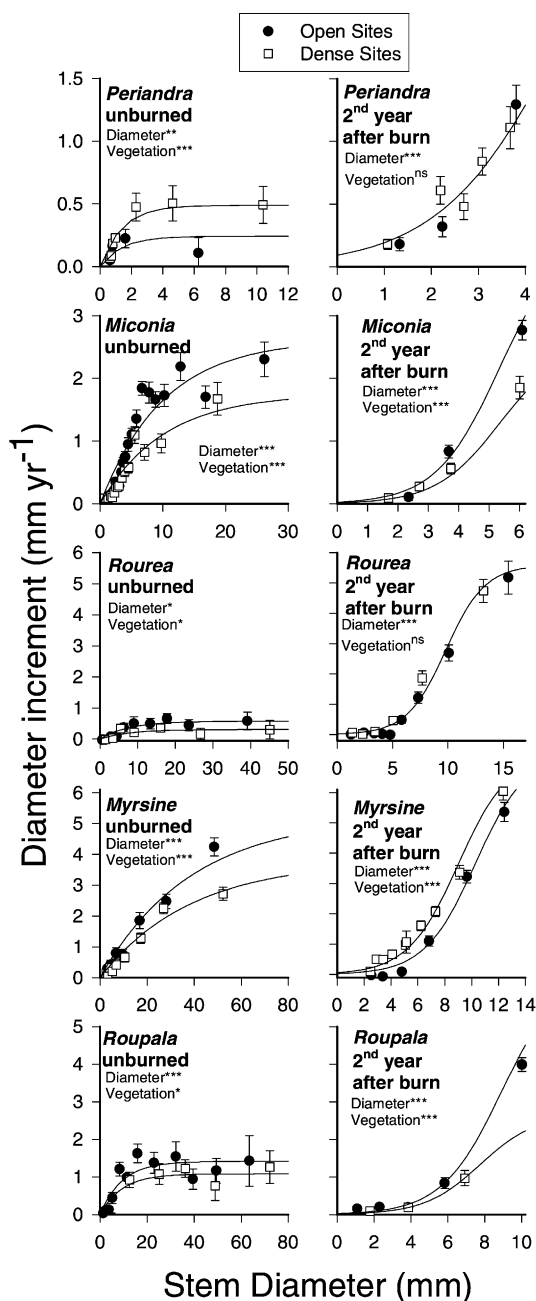


Fig. 6. The effect of vegetation density on diameter growth of five species. *Protium* and *Piptocarpha* are not shown because these were not significantly affected by vegetation density. The symbols and error bars represent the observed mean and standard error for groups of individuals. For *Periandra*, 25 individuals were included in each mean; for the remaining species, 50 individuals were included. The regression equations are provided in the Appendix A. Note the change in axes among graphs.

Table 3

Results of the ANCOVA to test for effects of phenological state (flush) on resprout diameter, after controlling for pre-burn diameter

Species	Error d.f.	F (flush)	P (flush)	F (diameter)	P (diameter)
<i>Roupala</i>	115	1.253	0.293	58.980	≤0.0001
<i>Rourea</i>	363	1.501	0.201	628.087	≤0.0001
<i>Periandra</i>	64	1.342	0.269	106.507	≤0.0001
<i>Protium</i>	124	1.434	0.227	73.051	≤0.0001

Phenological state did not affect resprout diameter for any of the species.

reduced stem diameter, confounding estimates of cambial growth.

Diameter growth of several species responded significantly to vegetation density. In unburned plots, growth was greater in the more open vegetation than in the savanna woodland for *Miconia*, *Myrsine*, *Roupala*, and *Rourea* (Fig. 6). Only *Periandra* exhibited higher growth rates in denser vegetation. In burned plots, the growth rate for the period beginning 1 year after burning was also greater in open than dense plots for *Miconia*, *Myrsine*, *Roupala*, and while *Periandra* and *Rourea* were unaffected by vegetation density and *Myrsine* had greater growth in dense vegetation (Fig. 6).

4. Discussion

Fire is shown here to have an important effect on cerrado woody plant demography through its impacts on survival, topkill, and growth. Fire increased mortality rates, though primarily among individuals with stem diameters less than 4 mm. While the consequences of increased mortality is rather straightforward because it represents a direct and immediate reduction in plant numbers, the effect of topkill has not received as much attention, perhaps because its impact on plant numbers is indirect. However, plant demography is more strongly determined by size than age (Harper, 1977; Solbrig, 1981), so a reduction in plant size due to topkill can have important consequences for future population growth (Hoffmann, 1999).

Although all individuals in the smallest size classes were topkilled by fire, a large fraction of these were able to regain their pre-burn size within 1 year after burning. For large individuals, however, topkill

represents a considerable loss of plant biomass that is not quickly regained. Once a tree or large shrub is topkilled by savanna fire, it becomes increasingly susceptible to topkill in subsequent fires due to this reduction in size. In fact, for those plots that burned twice in the study period, all individuals topkilled in the first fire were topkilled in the subsequent fire, regardless of whether 1 or 2 years elapsed between burns.

There is a particularly critical range of pre-burn diameter, from approximately 10 to 20 mm, within which few or no individuals are capable of regaining their pre-burn size within 1 year of burning (Fig. 5). These individuals are too small for their stems to avoid topkill, yet are too large to be able to regain their original size quickly. This critical range of stem diameters probably presents a severe limitation for many species under frequent burning. If the minimum reproductive size for a species is considerably greater than this critical diameter, there is likely to be little, if any, recruitment of individuals into reproductive size classes under frequent burning.

The subshrubs reach sexual maturity at a much smaller size than do the trees, so post-burn reproduction of subshrubs will be less strongly affected by topkill. Within 1 year of burning, large individuals of both subshrub species produced resprouts exceeding the minimum reproductive size. In contrast, the largest resprouts of the three tree species were only 20–37% of the minimum reproductive size. Of the two shrub species, large resprouts of *Rourea* exceeded the minimum reproductive size whereas large resprouts of *Miconia* were 85% of the minimum reproductive size. The three tree species, as well as *Rourea* and *Protium*, are capable of clonal spread via root suckers (Hoffmann, 1998), so individuals of these species do not necessarily need to attain sexual maturity to contribute to population growth. However, for the majority of cerrado tree and shrub species, there are no data to indicate the ability for clonal spread. The large incidence of vegetative reproduction among these study species probably reflects the choice of common species, since burning probably favors clonal species (Hoffmann, 1998).

The tendency of frequent fires to prevent recruitment to larger size classes has been noted in other systems (Rebertus et al., 1993). However, the low growth of cerrado trees make this problem particularly

acute here. In unburned plots, no species maintained mean growth rates greater than 2 mm per year for individuals within this critical size range (10–20 mm), suggesting that several years would be necessary for resprouts to reach sufficient size to avoid topkill. And although resprouts do have higher growth rates than plants in unburned areas, even if these high post-burn growth rates are maintained in subsequent years, several years would be required for them to reach a size at which they can reliably avoid topkill. But these higher post-burn growth rates may not continue in subsequent years, particularly if this early growth is maintained by carbohydrate reserves that are depleted by the early regrowth.

These data indicate that in the absence of a prolonged fire-free interval, few trees may be able to recruit into large size classes. While only a small fraction of the tree and shrub flora of the cerrado was studied here, these trends are supported by observations at the community level. During two fire cycles of 2 years each, Sato (1996) found that in an area initially encompassing 1212 trees with stem diameter greater than 5 cm, only 37 new individuals had recruited into this minimum stem diameter. This contrasts to 277 individuals that died within this same interval and a certainly larger number of individuals that regressed to smaller size classes, though this number was not reported. These, and other effects of repeated fire result in large changes in structure and species composition (Moreira, 2000).

While topkill exerts a serious constraint on tree populations, smaller growth forms will be less strongly affected. Indeed, in the cerrado, fire has a greater negative effect on densities of tree species than shrub species, while subshrubs tend to be favored by frequent burning (Hoffmann and Moreira, in press).

In some tropical savannas, increases in tree cover have been observed under annual burning (Silva et al., 2001; Dauget and Menaut, 1992 as cited by Hochberg, 1994). If the study species examined here are representative of cerrado species, increases in tree cover appear unlikely under annual burning. However, the data presented here were pooled from a range of fire intervals (1–21 years) and intensities, and therefore may not represent the specific case of annual burning. Specifically, due to low fuel availability, annual savanna fires are more likely to be patchy and of low intensity, which would change the relationship

between stem diameter and topkill. The lower intensity would permit smaller individuals to escape topkill, thereby narrowing the critical range in which no individuals are capable of regaining the pre-burn diameter. Nevertheless, Fig. 5 includes data from two plots burned in consecutive years and four other plots with low-intensity burns, so it is unlikely that the reduced intensity under annual burning would be sufficient to permit recruitment into large size classes, except perhaps for *Piptocarpha*.

For *Piptocarpha*, some individuals in every size class were able to retain or regain the pre-burn size within 1 year of burning, unlike the other species (Fig. 5). This was possible for this species because of its rapid regrowth following burning (Fig. 4). Interestingly, it is one of only two tree species (of 53 studied) that was significantly more abundant in frequently-burned than unburned sites (Moreira, 2000). This may be explained by the rapid regrowth, combined with its fire-stimulated flowering and capacity for clonal spread (Table 4) (Hoffmann, 1998). Several shrub species are also favored by frequent burning (Moreira, 2000), including *Rourea* which also exhibits relatively high regrowth rates (Table 4). While these results suggest the importance of rapid regrowth for success under frequent burning, detailed information on a larger subset of cerrado species is necessary to confirm this.

Canopy thinning due to tree death and topkill may have other effects by feeding back onto plant survival and growth. This response to density was clearest in unburned plots, and in burned plots for years in which burning did not occur. For *Myrsine*, *Miconia*, *Roupala*, and *Rourea* there was a clear negative effect of vegetation density on diameter growth in unburned plots. Two these species also responded negatively to vegetation density in the second year after burning. Cerrado savanna species are almost certainly shade-intolerant, as evidenced by their absence in nearby gallery forest (Felfili and Silva, 1992), which has a denser canopy than the cerrado woodland sites studied here. While cerrado may not be dense enough to exclude the study species, it is dense enough to reduce diameter growth, as has already been observed for *Roupala* and *Myrsine* (Hoffmann, 2002).

Contrary to predictions, individuals in a more advanced state of leaf flush at the time of burning did not exhibit lower regrowth rates than individuals in the initial stages of flushing, though others have found trees to be more sensitive to fire at the beginning of the growing season (Glitzenstein et al., 1995). In the current study, however, sample sizes were much smaller than for the other factors tested here.

Topkill and mortality tended to be significantly greater in high-intensity burns than in low-intensity burns, as has been shown in other savannas (Trollope,

Table 4
Summary of the fire traits of the seven study species

Species	Growth form	Resprout rate	Clonal spread ^a	Effect of fire on		
				Seed production ^a	Seedling establishment ^b	Population density ^c
<i>Periandra</i>	Subshrub	Low	No	–	–	–
<i>Protium</i>	Subshrub	Medium	Yes	?	?	0
<i>Miconia</i>	Shrub	Low	No	–	–	–
<i>Rourea</i>	Shrub	High	Yes	–	0	+
<i>Myrsine</i>	Tree	Medium	Yes	–	–	–
<i>Roupala</i>	Tree	Medium	Yes	–	–	–
<i>Piptocarpha</i>	Tree	High	Yes	+	?	+

For fire effects symbols are: (+) positive effect, (–) negative effect, (0) no effect, (?) no data. Fire effects on population density were obtained comparing density in frequently-burned site (approximately 2-year fire interval) with unburned sites (Moreira, 2000). Resprout rates were based on the asymptotic resprout rates provided by the equations in Fig. 3. These diameter growth rates were classified arbitrarily as low (<7 mm per year), medium (7–9 mm per year), and high (>9 mm per year).

^a From Hoffmann (1998).

^b From Hoffmann (1996).

^c From Moreira (2000).

1996; Williams et al., 1999). Savanna fires are most intense late in the dry season (Gill et al., 1996; Williams et al., 1998), the time when most burning currently occurs in the cerrado. These burns almost certainly have a larger impact on tree populations than burns in the wet season when most natural fires occur (Ramos-Neto and Pivello, 2000). Furthermore, fire frequencies are now almost certainly higher than prior to human occupation of the cerrado, compounding the impacts of humans on this ecosystem.

Appendix A. Regression equations describing plant responses to fire

A. Logistic regression equations of mortality where M is annual mortality, and LD is \log_{10} of stem diameter. For species in which only a single equation is presented, there was no significant difference between control and burn treatments. The R^2 statistic presented is Nagelkerke's R^2 .

<i>Miconia</i>	
Control	$M = 0.880/(1 + \exp(2.233 + 7.692 \text{ LD})) + 0.008; R^2 = 0.28$
Burn	$M = 0.934/(1 + \exp(-1.076 + 9.773 \text{ LD})) + 0.066; R^2 = 0.55$
<i>Myrsine</i>	
Control	$M = 1/(1 + \exp(1.117 + 3.806 \text{ LD})); R^2 = 0.21$
Burn	$M = 0.989/(1 + \exp(-0.011 + 5.194 \text{ LD})) + 0.011; R^2 = 0.13$
<i>Roupala</i>	
Control	$M = 0.136/(1 + \exp(-2.146 + 8.453 \text{ LD})) + 0.068; R^2 = 0.16$
Burn	$M = 0.532/(1 + \exp(-1.793 + 9.084 \text{ LD})) + 0.030; R^2 = 0.21$
<i>Periandra</i>	
Control	$M = 1/(1 + \exp(2.6443 + 3.0451 \text{ LD})); R^2 = 0.12$
Burn	$M = 0.953/(1 + \exp(2.331 + 13.237 \text{ LD})) + 0.047; R^2 = 0.35$

Appendix A. (Continued)

<i>Rourea</i>	
Control	$M = 0.478/(1 + \exp(2.564 + 4.030 \text{ LD})) + 0.009; R^2 = 0.07$
Burn	$M = 0.977/(1 + \exp(3.252 + 3.888 \text{ LD})) + 0.023; R^2 = 0.01$
<i>Piptocarpha</i>	
All treatments	$M = 1/(1 + \exp(0.614 + 4.065 \text{ LD})); R^2 = 0.17$
<i>Protium</i>	
All treatments	$M = 1/(1 + \exp(1.342 + 4.076 \text{ LD})); R^2 = 0.14$

B. Logistic regression equations of stem topkill. Fire intensity had a significant effect on topkill for all species. The R^2 statistic presented is Nagelkerke's R^2 .

<i>Miconia</i>	
Low intensity	$M = 1/(1 + \exp(-11.551 + 6.873 \text{ LD})); R^2 = 0.52$
High intensity	$M = 1; R^2 = 0.00$
<i>Myrsine</i>	
Low intensity	$M = 1/(1 + \exp(-13.585 + 8.546 \text{ LD})); R^2 = 0.57$
High intensity	$M = 1/(1 + \exp(-22.120 + 12.009 \text{ LD})); R^2 = 0.69$
<i>Roupala</i>	
Low intensity	$M = 1/(1 + \exp(-12.476 + 7.492 \text{ LD})); R^2 = 0.64$
High intensity	$M = 1/(1 + \exp(-12.197 + 6.602 \text{ LD})); R^2 = 0.55$
<i>Rourea</i>	
Low intensity	$M = 1/(1 + \exp(-20.056 + 12.752 \text{ LD})); R^2 = 0.61$
High intensity	$M = 1/(1 + \exp(-19.037 + 11.141 \text{ LD})); R^2 = 0.58$
<i>Piptocarpha</i>	
Low intensity	$M = 1/(1 + \exp(-11.704 + 7.058 \text{ LD})); R^2 = 0.64$
High intensity	$M = 1/(1 + \exp(-13.464 + 6.856 \text{ LD})); R^2 = 0.54$

C. Least-squares nonlinear regression equations describing diameter increment in unburned open (campo sujo and cerrado *sensu stricto*) and dense (cerradão) sites. For species in which only a single equation is presented, there was no significant difference between open and dense sites.

<i>Miconia</i>	
Open	$I = 2.622(1 - \exp(-0.099 D));$ $r^2 = 0.64$
Dense	$I = 1.755(1 - \exp(-0.099 D));$ $r^2 = 0.44$
<i>Myrsine</i>	
Open	$I = 5.226(1 - \exp(-0.026 D));$ $r^2 = 0.66$
Dense	$I = 3.790(1 - \exp(-0.026 D));$ $r^2 = 0.59$
<i>Rourea</i>	
Open	$I = 0.575(1 - \exp(-0.129 D));$ $r^2 = 0.12$
Dense	$I = 0.306(1 - \exp(-0.129 D));$ $r^2 = 0.05$
<i>Roupala</i>	
Open	$I = 1.414(1 - \exp(-0.107 D));$ $r^2 = 0.31$
Dense	$I = 1.081(1 - \exp(-0.107 D));$ $r^2 = 0.24$
<i>Periandra</i>	
Open	$I = 0.242(1 - \exp(-0.712 D));$ $r^2 = 0.17$
Dense	$I = 0.489(1 - \exp(-0.712 D));$ $r^2 = 0.41$
<i>Piptocarpha</i>	
All vegetation	$I = 1.657(1 - \exp(-0.053 D));$ $r^2 = 0.24$

D. Least-squares nonlinear regression equations describing diameter increment in the second year after burning in open (campo sujo and cerrado *sensu stricto*) and dense (cerradão) sites. For species in which only a single equation is presented, there was no significant difference between open and dense sites.

<i>Miconia</i>	
Open	$I = 4.354/(1 + \exp(5.125 - 0.956 D));$ $r^2 = 0.86$
Dense	$I = 2.580/(1 + \exp(5.125 - 0.956 D));$ $r^2 = 0.54$
<i>Myrsine</i>	
Open	$I = 7.317/(1 + \exp(5.456 - 0.531 D));$ $r^2 = 0.23$
Dense	$I = 7.317/(1 + \exp(4.794 - 0.531 D));$ $r^2 = 0.69$
<i>Roupala</i>	
Open	$I = 6.472/(1 + \exp(5.524 - 0.623 D));$ $r^2 = 0.79$
Dense	$I = 2.660/(1 + \exp(5.138 - 0.663 D));$ $r^2 = 0.45$
<i>Rourea</i>	
All vegetation	$I = 5.583/(1 + \exp(5.542 - 0.564 D));$ $r^2 = 0.55$
<i>Periandra</i>	
All vegetation	$I = 5.174/(1 + \exp(6.220 - 0.410 D));$ $r^2 = 0.76$

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