SHORT COMMUNICATION

Direct and indirect effects of fire on radial growth of cerrado savanna trees

WILLIAM A. HOFFMANN

Departamento de Engenharia Florestal, Universidade de Brasília, Caixa Postal 04357, Brasilia, DF 70919-970, Brazil

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Fire is the most prevalent form of disturbance in the cerrado savannas of south-central Brazil, commonly occurring at 2- to 3-y intervals (Coutinho 1990). Frequent fires are known to increase tree mortality (Sato & Miranda 1996), but it is unclear how they affect the growth of the surviving trees. Damage to the crown from scorching is likely to have a direct negative effect on plant growth, however the reduction in tree density due to repeated burning could indirectly stimulate growth because of release from competition. Understanding the relative strength of these contrasting direct and indirect effects of fire on tree growth is important for predicting human impacts on the cerrado vegetation.

Here I compare the direct negative effects and indirect positive effects of fire on tree growth in cerrado savanna by testing the effects of burning and tree density on the growth of two common tree species, *Myrsine guianensis* Aubl. (Myrsinaceae) and *Roupala montana* Aubl. (Proteaceae). In addition, seasonal patterns of radial stem growth were also studied for these species and for two other common species, *Rourea induta* Planch. (Connaraceae) and *Piptocarpha rotundifolia* (Less.) Baker (Compositae), however I did not compare the effects of fire and cover for these latter species. All four species are evergreen in that they retain leaves throughout the year, but there is typically some leaf loss during the dry season. Some individuals may lose all of their leaves by the end of the dry season, particularly in the case of *R. induta*.

Email: hoffmann@unb.br

In May 1993, individuals of the four species were located 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, and the adjacent Jardim Botânico de Brasília. The fire project consisted of 30 plots of 4–10 ha, subjected to different fire regimes or left unburned, with all plots having been previously unburned for at least 7 y prior to the experimental burns studied here. For *R. induta* and *P. rotundifolia*, three individuals were chosen in unburned cerrado. For *M. guianensis* and *R. montana*, 55 and 59 individuals were located throughout the fire project, distributed in a 3 × 2 factorial design. The factors include time since fire (unburned, burned in the previous year, and burned at the beginning of the study period) and vegetation density (cerrado *sensu stricto* and cerradão woodland). Cerradão woodland has a nearly closed canopy due to a greater density and a greater mean size of trees than cerrado *sensu stricto*, which is a savanna vegetation composed of a continuous grass layer with a discontinuous tree and shrub layer. I will subsequently refer to cerradão and cerrado *sensu stricto* as dense and open sites, respectively.

Differences in edaphic characteristics between cerrado *sensu stricto* and cerradão at the site are minimal, with the cerradão soils having 8% more P and 28% more K than cerrado *sensu stricto*, and no differences in pH, Ca, Mg, Al, organic matter, or sand/silt/clay fractions (Moreira 2000). The study site is not unique in this aspect, as cerradão and cerrado *sensu stricto* soils commonly exhibit little or no difference in nutrient availability (Haridasan 1992).

A dendrometer was used to measure monthly rates of stem diameter growth, as described by Daubenmire (1945). To permit the measurements, three brass screws were placed in the tree trunk at 30 cm height and a small aluminium plate was glued to the tree trunk between these screws. The dendrometer measures the displacement of this plate relative to the screws. Due to minimum size requirements for this method, only individuals with stem diameter larger than 80 mm at 30 cm height were included in this study. Measurements were performed on approximately the 15th day of every month from May 1993 to July 1994, always within an hour of sunrise to avoid problems associated with daily fluctuations in stem diameter resulting from changes in plant water status. Growth increments were multiplied by 2 to obtain diameter growth. Notes were taken on the occurrence of leaf flushing of each plant during these monthly measurements.

Radial stem growth of all four species closely tracked seasonal patterns of precipitation, with peak growth occurring in the middle of the wet season and little or no growth occurring in the dry season (Figure 1). Peak growth did not correspond to the timing of leaf flush as is typical in temperate regions (Kozlowski *et al.* 1991). Instead, there was a lag of approximately 2 mo between the beginning of leaf flush and the onset of rapid radial growth (Figure 1). Similar patterns have been observed in other species of the seasonal tropics,
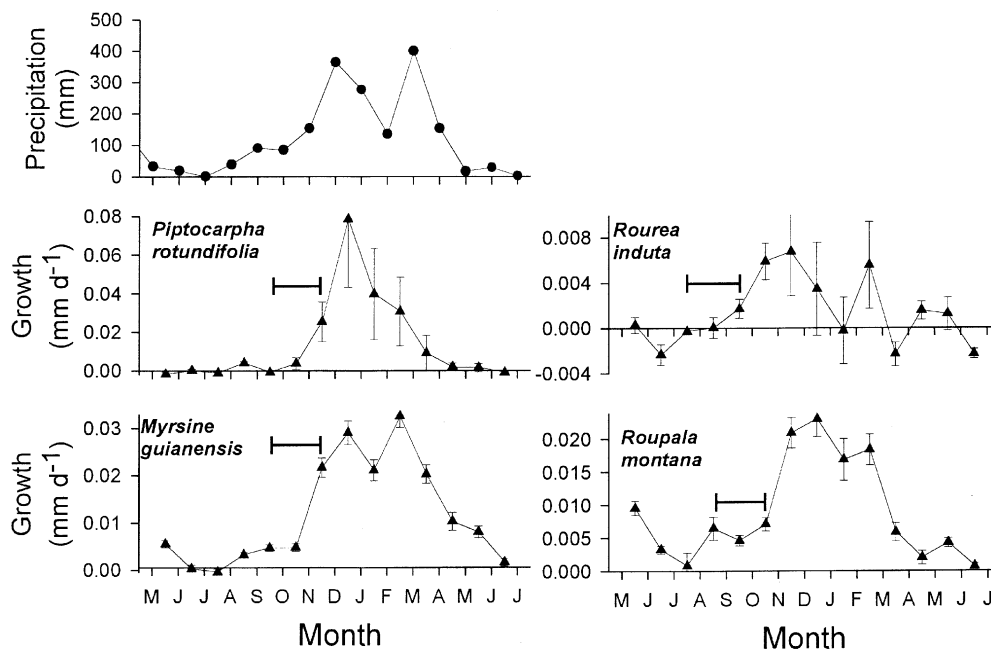
Figure 1. Seasonal pattern of precipitation and growth in stem diameter (mean ± SE) pooled over all treatments. The horizontal bar indicates months in which at least 50% of the individuals were producing new leaves. In all cases, peak radial stem growth occurred at least 2 mo after leaf production began. Tick mark location on the horizontal axis corresponds to the midpoint of a particular month.

where xylem production was found to lag two or more months behind leaf flush (Ajmal & Iqbal 1987, Iqbal & Ghouse 1985).

Roupala montana and other cerrado trees are known to maintain high rates of transpiration and photosynthesis throughout the dry season (Franco 1998, Jackson *et al.* 1999, Meinzer *et al.* 1999). The carbon fixed by these plants at this time was apparently not used to sustain shoot growth or leaf production, as these activities ceased during most of the dry season. Root growth and storage may be important sinks for the photosynthate fixed at this time.

For *M. guianensis* and *R. montana*, annual radial stem growth differed significantly among fire treatments (Figure 2; Table 1). Orthogonal contrasts indicated that growth was significantly lower in recently burned plants than in plants burned one or more years previously ($F_{1,102} = 6.02$, P = 0.016), but there was no difference between plants burned one year previously and plants burned seven or more years previously ($F_{1,102} = 0.433$, P = 0.512). Therefore, growth rates were reduced in the first year after burning, but had recovered to preburn rates by the following year. Although there was a net reduction in growth, it seems likely that the short-term release of nutrients following burning (Kauffman *et al.* 1994) could have contributed a positive effect, but any such effect was hidden by the larger negative effect which was probably caused by damage to the crown. The loss of photosynthetic area and the subsequent
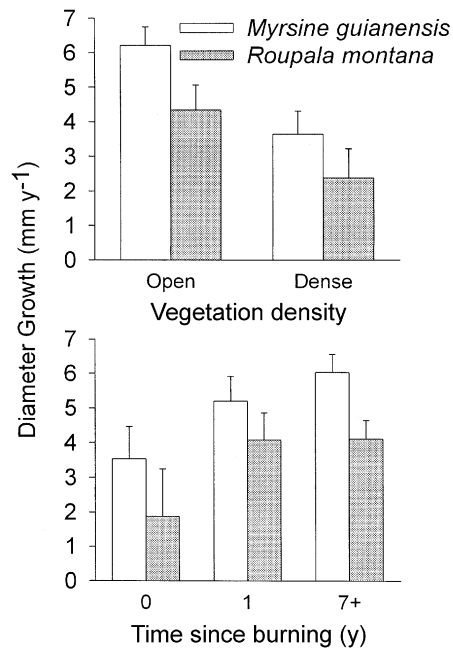
Figure 2. The effect of tree density and fire on annual stem diameter growth (mean ± SE) of *Myrsine guianensis* and *Roupala montana* from July 1993 to July 1994. There were significant effects of species ($F_{1,102} = 5.01$, $P = 0.027$), vegetation density ($F_{1,102} = 10.6$, $P = 0.002$), and burning ($F_{2,102} = 3.47$, $P = 0.035$) on radial growth, but no significant two-way or three-way interactions between these factors.

allocation of resources for crown regrowth are both likely to have contributed to this decline in growth.

In the longer term, however, fire may have a net positive effect on the radial growth of these species, particularly in denser formations. Radial growth was significantly higher in open sites than in dense sites (Figure 2; Table 1). Since fire tends to reduce vegetation density, the short-term effect of fire on radial growth may be offset by the positive effects resulting from the opening of the vegetation.

At the study site, it is unknown what factors are responsible for the spatial

Table 1. Analysis of variance testing the effects of species, vegetation density and time since burning on diameter growth.

Source of variation	df	MS	F	P
Species	1	10.98	5.05	0.026
Vegetation density	1	23.00	10.58	0.002
Time since burning	2	7.54	3.47	0.035
Species × Vegetation	1	0.41	0.19	0.663
Species × Time	2	0.42	0.19	0.826
Vegetation × Time	2	2.77	1.27	0.284
Vegetation × Time × Species	2	2.13	0.98	0.379
Error	102	2.17		

variation in vegetation density. If some factor other than fire is responsible for this variation, it is unlikely to be responsible for the observed density dependence of growth rates. For example, if the slightly lower nutrient availability in the open sites (Moreira 2000) were responsible for the lower tree cover, it would not explain the higher growth rates observed there. Similar arguments can be made for other factors that might determine tree density, such as soil depth or water availability. If there is some confounding between the effects of tree density and other factors on growth rate in this study, it is almost certain to have resulted in an underestimation, rather than an overestimation, of the density effects.

The effect of burning on radial growth was of approximately the same magnitude as the effect of tree density. Since the effect of burning is temporary, whereas density had an effect regardless of time since burning (non-significant time × vegetation interaction, Table 1), this suggests that only annual burning would have as negative an effect as dense vegetation. In short, the indirect positive effects of fire are larger than the direct negative effects.

This reasoning must be interpreted with caution for several reasons. First, the reduction in vegetation density tends to occur gradually as a result of repeated fires (Hoffmann 1999). Since the reduction in tree density from a single fire is expected to be small, the net positive effect on growth should also be small. Also, the results of this study apply only to large individuals. Small individuals are typically topkilled by fire (Gignoux *et al.* 1997), causing a large reduction in plant size that might never be offset by any positive effects of fire. Also, the effects of repeated fire may be much more severe than expectations based on the study of individual fires, since repeated fires may deplete carbohydrate and nutrient reserves necessary for postburn growth (Miyanishi & Kellman 1986), and can cause net loss of nutrients from the ecosystem. Finally, the effects of vegetation density on tree growth may be important only in the denser portion of the range of vegetation densities. If light availability was the primary factor limiting tree growth in the denser physiognomy, then changes in tree density may have little effect on tree growth within the more open forms of cerrado where shading is much less prevalent.

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