Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction

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Summary

1. Burning typically occurs at intervals of 1–3-years in the Brazilian cerrado, a rate that exceeds the precolonization fire regime. To determine if woody plants of the cerrado successfully reproduce within the short span of time between burns, experimental burns were used to quantify the effects of fire on sexual and vegetative reproduction of six species of resprouting trees and shrubs.

2. Four of the six species reproduce vegetatively by producing root suckers. For three of these species, *Rourea induta*, *Myrsine guianensis* and *Roupala montana*, sucker production was seven to 15 times greater in burned plots than in unburned controls.

3. Fire had a negative impact on sexual reproduction. Fire caused an immediate reduction in sexual reproductive success by destroying developing reproductive structures and seeds. Additionally, five of the six study species exhibited overall reductions in seed production in the years following fire. Fire had this effect by reducing the individual size of all species and, for three species, by reducing size-specific reproductive output. Only the tree *Piptocarpha rotundifolia* exhibited increased seed production following burning.

4. Fire caused substantial mortality to both seedlings and suckers. Suckers were larger than seedlings and experienced lower mortality rates for two of three species. Fire-induced mortality of seedlings varied greatly among species, ranging from 33% to 100%.

5. The results indicate that vegetative reproduction is much more successful than sexual reproduction under the high fire frequency typical of current fire regimes. It is concluded that current fire regimes must be causing a shift in species composition, favouring species capable of vegetative reproduction.

Key-words: cerrado, fire, seedlings, shrub, tree.

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Introduction

Humans have had a large impact on the dynamics of many ecosystems by altering fire frequencies (Bond & van Wilgen 1996). This has been particularly true in the savannas of the Brazilian cerrado, where fire now typically occurs at intervals of 1–3 years (Eiten & Goodland 1979; Coutinho 1990) primarily due to anthropogenic causes. Similar fire frequencies are currently typical of tropical moist savannas of Australia, Africa and Asia (Lacey, Walker & Noble 1982; Trol-

lope 1984; Stott 1990; Menaut *et al.* 1991; Russell-Smith, Ryan & Durieu 1997). In the cerrado, it is uncertain what range of fire frequencies was typical prior to European colonization, but it has been estimated that burning intervals ranged from 3 to 10 years under indigenous occupation (Ratter *et al.* 1973; Eiten 1975; Eiten & Goodland 1979).

Frequent burning can be a major constraint for reproduction of woody plants. For a species to reproduce successfully sexually, seedlings must establish and grow to fire-tolerant size within the short period of time between burns. Furthermore, if the species lacks a mechanism to protect seeds from burning, then flowering and seed maturation must also occur prior to seedling establishment. If fire recurs before it is

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possible to complete this entire sequence from flowering to establishment of fire-tolerant seedlings, reproduction is curtailed (Bradstock & Myerscough 1988). In the cerrado, some species exhibit mechanisms to protect seeds from burning (Coutinho 1977a; Landim & Hay 1996) but many do not. Therefore, successful sexual reproduction under frequent fire must be contingent upon rapid post-burn flowering and early fire tolerance of seedlings.

Even if burning is too frequent to permit successful sexual reproduction, vegetative reproduction may be successful. The cost of vegetative reproduction can be lower than sexual reproduction (Abrahamson 1980), reducing the constraints on post-burn vegetative reproduction. Also, vegetative offspring tend to be larger than seedlings of similar age and have a greater capacity to survive environmental stress (Abrahamson 1980), so fire tolerance might be attained sooner (Peterson & Jones 1997). Many woody species of the cerrado are known to reproduce vegetatively via root suckers or rhizomes (Rawitscher, Ferri & Rachid 1943; Ferri 1962; Rizzini & Heringer 1962; Raw & Hay 1985) but the importance of vegetative reproduction relative to sexual reproduction is unknown.

Understanding the effects of burning on reproduction is necessary for predicting the long-term effects of current fire regimes on woody plants of the cerrado, and was recently identified as a priority area of research for developing management guidelines in the cerrado (Pivello & Norton 1996) and other tropical savannas (Solbrig *et al.* 1992). If current fire regimes are having a negative impact upon reproduction, it cannot be assumed that the effects on the cerrado would be immediately evident. Woody plants of the cerrado resprout vigorously following burning, so they are not dependent upon frequent reproduction for short-term population maintenance. Additionally, individual growth rates are low, so changes in reproductive success could require decades to have an impact on the density of adult woody plants. Understanding the effects of burning on reproduction could reveal if attrition of plant populations is occurring under current fire frequencies.

In this study, the effects of burning on the reproduction of six woody plant species of the cerrado, including three trees, two shrubs and one subshrub, were examined. Post-burn seed and sucker production, as well as the effect of fire on offspring survivorship, was quantified to answer two questions. (i) Are woody plants of the cerrado able to reproduce successfully under current fire regimes? (ii) How does fire affect the relative importance of sexual vs. vegetative reproduction?

To avoid confusion, it must be noted that the term 'root sucker' will refer to a new stem originating from a root bud at some distance from the parent stem. Sprouts originating from the root crown or stem base will not be referred to as suckers. As adults, all species studied here resprout from the root crown following fire, but this will be referred to as survival rather than vegetative reproduction.

Methods

STUDY SPECIES AND SITE

Six study species were chosen to span the range of growth forms from subshrub to tree. The species included the subshrub *Periandra mediterranea* Taub. (Leguminosae); two shrubs, *Miconia albicans* Steud. (Melastomataceae) and *Rourea induta* Planch. (Connaraceae); and three trees *Myrsine guianensis* Aubl. (Myrsinaceae), *Piptocarpha rotundifolia* (Less.) Baker (Compositae) and *Roupala montana* Aubl. (Proteaceae). All are resprouting evergreen species, are abundant at the study site and are common throughout much of the cerrado (Ratter *et al.* 1996).

All research was conducted at the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE) and the adjoining Botanical Garden of Brasília (JBB). The site is located approximately 35 km south of Brasília, at 15°56′S and 47°53′W, with an elevation of 1100 m.a.s.l. Mean annual rainfall (1980–94) at the site is 1480 mm, of which 91% occurs in the summer months of October to April. Mean annual temperature (1980–94) is 21·8 °C. The soil at the site is dark red latosol of the Brazilian soil classification system, corresponding to oxisol of the US soil taxonomy system and ferralsol of the FAO system (Sanchez 1976). The soils are deep and well drained.

A large fire project is located at the site. The experimental area of the fire project is divided into 30 10-ha plots. Each plot is subjected to one of five fire regimes: (i) no burning; (ii) early-season biennial burning; (iii) mid-season biennial burning; (iv) late-season biennial burning; and (v) mid-season quadrennial burning. The season of burning refers to whether the plots are burned at the beginning (June), middle (August) or end (September) of the dry season. The plots burned at 4-year intervals were first burned in 1991. Of the plots burned at 2-year intervals, half were first burned in 1992 and the other half were first burned in 1993. Prior to these experimental burns, the plots had been unburned for 7 or more years.

QUANTIFYING VEGETATIVE REPRODUCTION

To quantify vegetative reproduction, 12 permanent study plots (15 × 25 m) were established within the fire project described above. Six plots were established in areas designated as unburned controls and six were established in areas scheduled to be burned at 2-year intervals late in the dry season. No two of these study plots were established within the same 10-ha plot of the fire project, ensuring independence among plots. Three plots of each of these two treatments were estab-

lished in the dry season of 1992 and the remaining plots were established in the dry season of 1993.

Within the plots, all individuals of the six study species were mapped, tagged and measured. For individuals with height greater than 60 cm, stem diameter was measured at a height of 30 cm. For smaller individuals, diameter was measured at one half the stem height. Censuses were conducted at yearly intervals from 1992 to 1995 in the dry season before any burning was performed.

Within each 15×25-m plot, a 5×15-m subplot was established, which was centred within the larger plot. At each census, all new suckers in this subplot were mapped, tagged and measured. Suckers were easily distinguished from seedlings due to the larger size of suckers and differences in morphology.

In some of the study species, the connection between adult and root sucker often disintegrates when the sucker is less than 1 year old. Because it was not possible to determine which adult in a population was the parent of a particular offspring, the method of Ribbens, Silander & Pacala (1994) was adapted to estimate sucker production as a function of individual size (see the Appendix). This method uses a maximum likelihood estimator to find the best fit to the allometric equation:

$$S = \alpha \cdot d^{\beta}$$

where d is stem diameter and S is the number of suckers produced. The parameters α and β are estimated by an iterative algorithm that finds the relationship which best predicts the densities of suckers in the study plots. The likelihood ratio test was used to test for effects of stem diameter and time since burning on the number of suckers produced. Pair-wise comparisons were performed using the Bonferroni adjustment of the significance level (Sokal & Rohlf 1995).

SEXUAL REPRODUCTION

Annual censuses were conducted to estimate seed production of the marked individuals in the 15×25-m plots described above. Additionally, temporary transects were established in other treatments of the fire project to increase the sample of adult individuals and to include samples from all the fire regimes represented by the fire project. The twelve 15×25-m permanent plots were not used for *Myrsine* because this species is dioecious and clonal, so the probability of producing fruit was not independent among adjacent individuals.

Sampling points were quantified at 5-m intervals along each transect, and the nearest individual of a particular study species was selected. Each transect was extended until a predetermined number of individuals of a species was sampled. These transects were established merely to supplement the data from the permanent plots, so sample sizes varied among species depending on how well a species was represented in the permanent plots (Table 1). Also, larger sample sizes were obtained for those species that had higher variation in seed output among individuals. In any given year, no more than one transect was established per experimental plot of the fire project to ensure independence, although transects were established in the same plots in different years. For *Rourea*, the timing of fruiting prevented sampling of areas burned 3 years previously in the years that censuses were performed.

Because of species differences, the protocol for estimating seed production differed among species. For *Periandra*, *Rourea* and *Myrsine*, a direct count of fruit was obtained. For *Miconia* and *Roupala*, inflorescences were counted. For *Piptocarpha*, capitula were usually directly counted. For tall individuals, it was not possible to count individual capitula, which occur in clusters in the leaf axils. For such cases, reproductive leaf axils were counted and then several branches were sampled to estimate a mean number of capitula per leaf axil. A whole tree estimate was obtained by multiplying these two values.

ANALYSIS OF SEXUAL REPRODUCTION

Many of the censused individuals produced no fruit, so it was not possible to transform the data to produce normally-distributed residuals. Therefore, the probability of fruiting was analysed separately from the number of fruit per fruiting individual. Logistic regression was used to determine what factors influenced the probability of fruiting. Then, analysis of covariance was used to determine what factors influenced the number of fruit produced per individual. Non-fruiting individuals were omitted from this second analysis. All analyses were performed with SYSTAT version 5·01 (Wilkinson 1990).

Many individuals failed to reproduce, even in the largest size classes, so a modified logistic regression equation was used:

$$p = k \frac{e^{a + b \cdot d}}{1 + e^{a + b \cdot d}}$$

where p is the probability of reproducing and d is stem diameter. The parameter k permits the regression line to asymptotically approach some value less than 1. This model was found to always have a significantly better fit than the model excluding the parameter k. The likelihood ratio test was employed to test for fire and diameter effects.

Analysis of covariance was used to test for effects of burning and stem diameter on fruit production of fruiting individuals. Plots were considered nested within burn treatments, and individuals were nested within plots. Stem diameter at the time of fruiting was included as a covariate. Thus for testing for fire effects, plots were considered to be the experimental unit rather than individuals. The Satterthwaite approxi-

Table 1. Summary of the sample sizes for sexual reproduction data in different fire treatments. Values presented are the number of individuals censused. The values in parentheses are the number of plot and transects from which these individuals were censused

| Species | Time since burning | | | |
	1 year	2 years	3 years	Unburned
Periandra mediterranea	380 (10)	353 (11)	120 (4)	550 (12)
Miconia albicans	339 (6)	517 (11)	40 (2)	3176 (12)
Rourea induta	578 (6)	151 (6)	0 (0)	524 (6)
Myrsine guianensis	120 (6)	135 (6)	80 (4)	110 (4)
Piptocarpha rotundifolia	504 (19)	234 (10)	41 (4)	414 (17)
Roupala montana	1534 (24)	641 (10)	40 (2)	2406 (26)

mation (Steele & Torrie 1980) was used to test for fire effects. Both stem diameter and reproductive output were transformed with the natural logarithm. Pairwise comparisons were performed using the Bonferroni adjustment of the significance level (Sokal & Rohlf 1995).

Both logistic regression and analysis of covariance test for an effect of burning on size-specific reproduction. Burning can also reduce reproduction by reducing individual size. This effect must be considered if we are to understand the overall effect of burning on seed production. Pre-burn was compared with post-burn reproduction, after adjusting for changes in individual size. Using stem-diameter data from the permanent plots, the effect of fire on individual size and subsequent regrowth was quantified. Then the regression equations from logistic regression and analysis of covariance were used to estimate reproductive output of pre-burn and post-burn individuals. An arbitrary pre-burn stem diameter must be chosen as a point of reference; the mean size of reproductive individuals was used arbitrarily as the reference. The method of Baskerville (1972) was used to eliminate the bias of estimates from the log-transformed regressions obtained from the analysis of covariance.

FIRE SENSITIVITY OF SEEDS, SEEDLINGS AND SUCKERS

Of the study species, only *Periandra* and *Myrsine* often disperse seeds in the dry season before burning occurs. To determine if these dispersed seeds survive burning, seeds were placed on the soil surface immediately prior to burning. Five seeds of each species were placed on the soil surface at 10 points at 5-m intervals along transects and the seeds collected following burning. One such transect was established in each of three experimental burns.

Cohorts of suckers produced within the permanent plots were monitored to quantify survival in burned and unburned plots. Similarly, cohorts of seedlings remaining from a separate study (Hoffmann 1996) and additional unpublished experiments were also monitored to quantify the effect of burning on seedling survival. Cohorts of seedlings were available for all species except *Piptocarpha*, for which there was no field germination. The number of seedlings available was dependent on seed availability and establishment success, but in every case the seedlings were distributed among a large number of study plots scattered throughout the fire project. The number of plots ranged from 36 for *Rourea*, to 68 or more for the remaining species. Cohorts of 3 separate years were available for *Myrsine*, *Periandra* and *Roupala*, of 2 years for *Miconia*, and of 1 year for *Rourea*.

Results

VEGETATIVE REPRODUCTION

Myrsine, *Piptocarpha*, *Rourea* and *Roupala* were found to produce root suckers, whereas *Miconia* and *Periandra* produced none. Burning increased sucker production for *Myrsine*, *Rourea* and *Roupala* (Fig. 1). In the year that burning occurred, sucker production was 7 to 14 times greater than in unburned plots, depending on the species. The stimulatory effect of fire continued into the second year following burning for *Roupala* and *Myrsine*, because more suckers were produced in the year after burning than in unburned populations (Fig. 1). All three species showed a significant positive relationship between stem diameter and sucker production ($P < 0.005$; Fig. 1).

Piptocarpha was too scarce in the study plots and produced too few suckers to be able to draw any conclusions regarding the effects of burning. A total of only 13 root suckers of this species was produced in the study plots during the study period.

SEXUAL REPRODUCTION

In the year that burning occurred, none of the study species successfully reproduced sexually. As is typical for most cerrado species, the fruit of the study species mature in the dry season or early in the wet season, so dry-season burning interrupted reproduction by
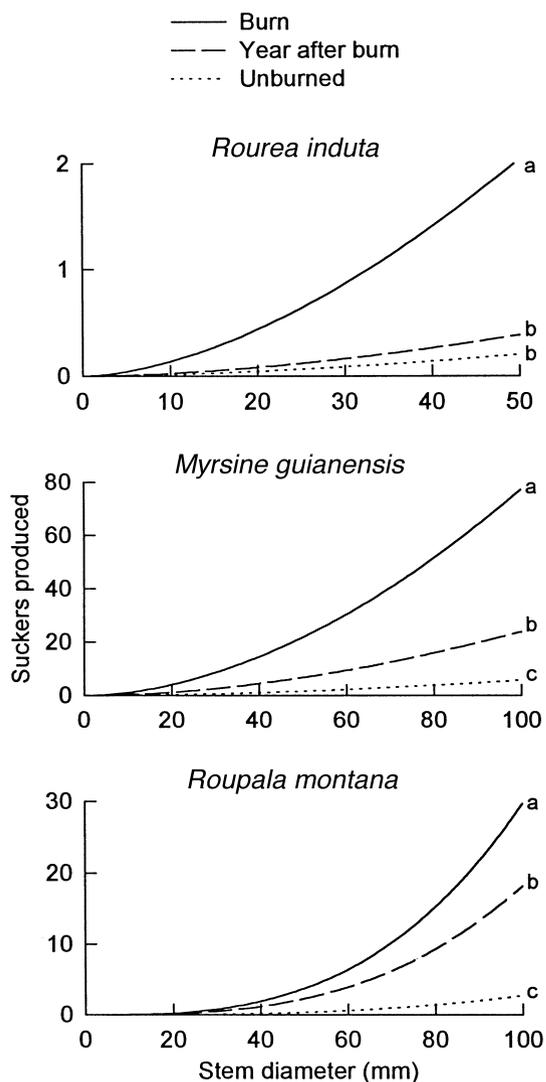
Burn
Year after burn
Unburned

Fig. 1. Effect of burning on the production of root suckers. The curves show the relationship between stem diameter and the numbers of suckers produced per individual, as determined by the maximum likelihood estimator described in the Appendix. Curves with the same letter were not significantly different after using the Bonferroni adjustment.

destroying flower buds, mature flowers, developing fruit or recently-dispersed seeds. Since none of the study species have mechanisms to protect these structures from heat, no viable seeds were ever observed to be available for germination in the first wet season following burning.

All seeds of *Myrsine* ($n = 150$) and *Periandra* ($n = 150$) placed on the soil surface prior to burning were destroyed by the fire. Although germination was not attempted, damage to the seeds was too complete for germination to be possible.

After the first year, the six study species varied greatly in the way in which flower/fruit production changed through time. Time since fire had no influence on the size-specific probability of reproducing for *Periandra*. For *Miconia*, the probability of reproducing dropped greatly in the first year following

burning, relative to other plots (Fig. 2). The only individuals reproducing in the first year were a few large individuals that were not killed back to ground level; no resprouting individuals reproduced at this time. Size-specific reproduction increased through the first 3 years following burning but eventually declined for long-unburned plots. For *Rourea*, the probability of reproduction peaked in the second year following burning, relative to unburned plots (Fig. 2). For *Myrsine* and *Roupala*, the probability of reproducing was greatly reduced in the first year following burning, gradually increasing in subsequent years (Fig. 2). *Piptocarpha* was the only species to exhibit an increase in the size-specific probability of reproducing in the first year following burning (Fig. 2). After the initial peak, the probability of reproducing returned to pre-burn levels.

All six species exhibited a significant positive relationship between stem diameter and probability of reproducing ($P < 0.005$; Fig. 2).

Qualitatively, the effect of fire on the number of fruit per reproducing individual was similar to the effect of fire on the proportion of individuals reproducing. However, fewer comparisons showed significant effects. Five of the six species exhibited highly significant positive relationships between stem diameter and reproductive output ($P < 0.005$). Only *Rourea* was marginally insignificant ($F_{1,100} = 3.89$, $P = 0.051$).

For *Periandra*, *Rourea* and *Roupala*, time since burning had no effect on size-specific reproductive output of reproducing individuals (Fig. 3). For *Miconia*, the number of inflorescences was lowest 1 year after burning, increasing in subsequent years, and eventually declining for unburned plots (Fig. 3). For *Myrsine*, fruit production was lowest in recently-burned plots and increased with time since burning (Fig. 3). For *Piptocarpha*, the number of capitula produced in the first year following burning was significantly greater than in other treatments (Fig. 3).

Overall, burning reduced post-burn reproduction for five of the six study species (Fig. 4). This overall effect of burning incorporated the effect of burning on size-specific probability of reproducing, the effect of burning on the size-specific seed production of reproducing individuals, and the effect of burning on individual size. For these species, lowest seed production is observed 1 year after burning, increasing monotonically in subsequent years. Only *Piptocarpha* truly exhibited fire-stimulated reproduction (Fig. 4).

For *Periandra*, the mean number of entire seeds per fruit was 1.90 ± 0.06 (mean $\pm$ SE, $n = 1616$) across all treatments. *Miconia* produced 27.4 ± 1.3 (mean $\pm$ SE, $n = 473$) fruit per inflorescence and 23.6 ± 0.6 (mean $\pm$ SE, $n = 137$) seeds per fruit. *Piptocarpha* produced 3.15 ± 0.05 (mean $\pm$ SE, $n = 1188$) seeds per capitulum. In 1994, only 2·6% of the seeds were potentially viable, the remainder were empty. In 1993, no viable seeds were found. For
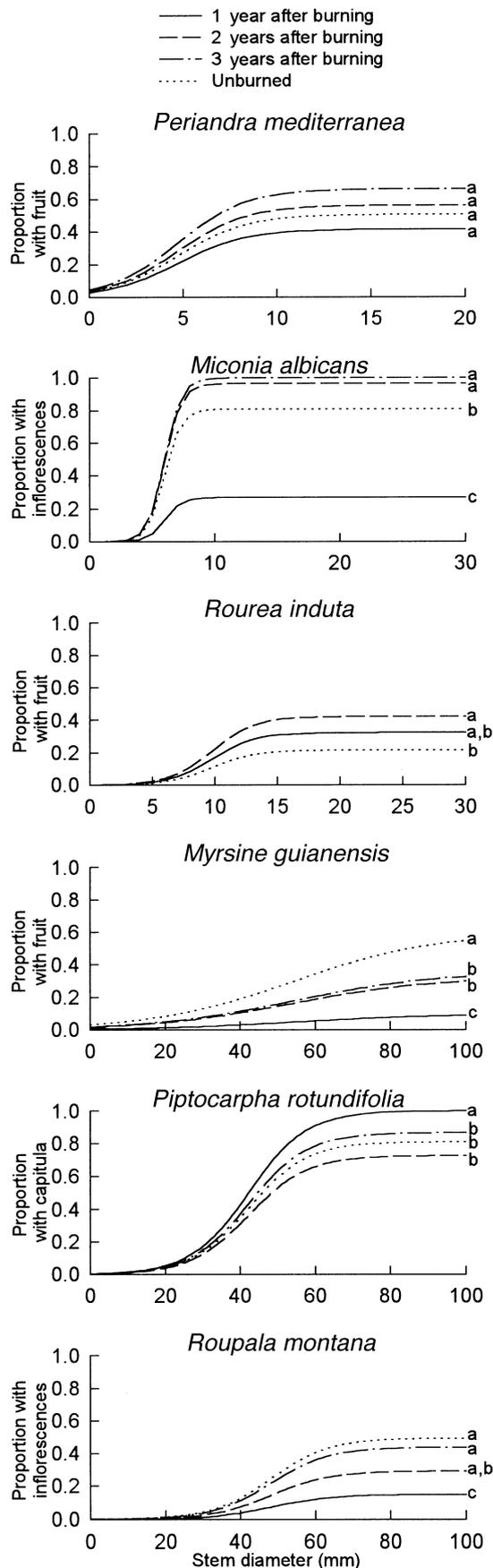
Fig. 2. Probability of producing fruit as a function of stem diameter and time since burning. The curves were obtained with logistic regression as described in text. Curves with the same letter were not significantly different after using the Bonferroni adjustment.

Rourea and *Myrsine*, which produce single-seeded fruits, 24·8% and 30·0% of the seeds were entire, respectively. For *Roupala*, which produces up to two seeds per fruit, the mean number of entire seeds per fruit was 0·73 ($n = 2136$), and the number of fruit per inflorescence was $1·43 \pm 0·04$ (mean $\pm$ SE, $n = 4897$). Seed parasites destroyed a large number of seeds of *Periandra*, *Rourea* and *Roupala* but the other species were not heavily parasitized. Parasitized seeds were not included in the counts of seed per fruit.

SURVIVAL OF OFFSPRING

Mortality of offspring was calculated for the 1-year period commencing at the start of the first dry season. Burning significantly increased mortality of seedlings for *Miconia*, *Roupala*, *Periandra* and *Myrsine* (Fig. 5). *Miconia* was the only species to suffer 100% seedling mortality from burning. Two-year-old seedlings of this species also exhibited 100% mortality as a result of burning (data not shown).

Burning increased mortality of suckers for *Myrsine* and *Roupala* (Fig. 5). Burning did not affect mortality of seedlings or suckers of *Rourea* (Fig. 5); however, sample sizes were too small to test adequately for differences.

The stem diameters of seedlings were smaller than those of suckers for *Myrsine*, *Rourea* and *Roupala* (Table 2). For *Myrsine*, suckers had higher survivorship than seedlings in burned ($G_1 = 12·96$, $P = 0·0003$) and unburned plots ($G_1 = 10·99$, $P = 0·0009$). Suckers of *Roupala* also had higher survivorship than seedlings in burned plots ($G_1 = 5·37$, $P = 0·02$) but not in unburned plots ($G_1 = 0·27$, $P = 0·60$). Burning reduced survivorship of seedlings more than it reduced survivorship of suckers. For *Roupala*, burning caused a 56% reduction in seedling survival but only a 21% reduction in sucker survival. For *Myrsine*, burning caused a 74% reduction in seedling survival but only a 34% reduction in sucker survival.

Discussion

For the study species, burning tended to increase the importance of vegetative reproduction relative to sexual reproduction. This resulted from reductions in sexual reproduction and increases in vegetative reproduction, as well as greater fire tolerance of vegetatively produced offspring relative to sexually produced offspring.

Burning had a net negative effect on sexual reproduction in five of the six study species, due to several contributing factors. First, none of the study species successfully produced seed in the year that burning occurred. Depending on the phenology of the species and the time of burning, fire destroyed dispersed seeds, developing fruit or flower buds. This effect alone can greatly reduce the mean annual seed production under
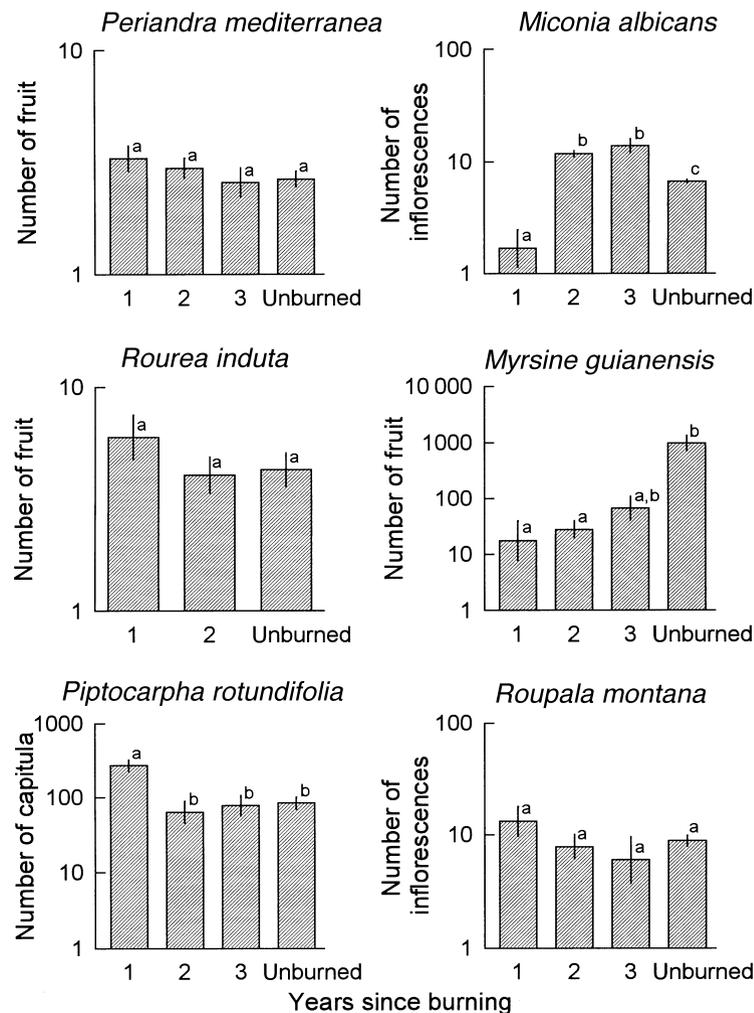
Fig. 3. Effect of burning on the number of fruit or inflorescences per reproducing individual. Non-reproducing individuals were not included in this analysis. Values shown are means ($\pm$SE), adjusted for stem diameter using analysis of covariance. Treatments with the same letter were not significantly different after using the Bonferroni adjustment.

frequent burning, destroying the entire seed crop in any year burning occurs. Secondly, another cause of reduced sexual reproduction is lower size-specific reproductive output in the years following burning. For *Miconia*, *Myrsine* and *Roupala*, size-specific seed production was lower in recently burned plots than in unburned plots. However, for the three other species, the effect of fire on size-specific seed production was positive or non-significant. Thirdly, reduced individual size caused additional reduction in post-fire seed production. When the effect of burning on seed production was adjusted to include the negative effect of fire on individual size, all species exhibited declines in seed production in response to burning, except for *Piptocarpha*. Finally, sexual reproductive success is further reduced by the effect of fire on seedling survival. Fire significantly increased seedling mortality of four of five species.

There was no clear relationship between growth form and ability to reproduce sexually following burning (Table 3). However, it must be noted that fire

stimulates flowering in many subshrubs of the cerrado (Coutinho 1977b), so *Periandra*, the only subshrub studied here, is not representative of this growth form.

The data obtained here can be used to estimate the minimum fire interval that permits sexual reproduction. For example, *Periandra* and *Rourea* may reproduce sexually under biennial burning because they both produce seeds 1 year after burning and the seedlings of these species are relatively fire tolerant. On the other hand, *Myrsine* and *Roupala* should have very limited sexual reproductive success under biennial burning. Both species produce few seeds the year after burning and their seedlings are more fire sensitive than the previous two species, so more than 2 years are needed for substantial sexual reproduction to occur. *Miconia* produces virtually no seeds one year after burning and has seedlings that are unable to survive burning until at least 3 years of age, so this species requires at least 5 years between successive burns for successful sexual reproduction. Of the two species unable to reproduce vegetatively, *Periandra* is able to
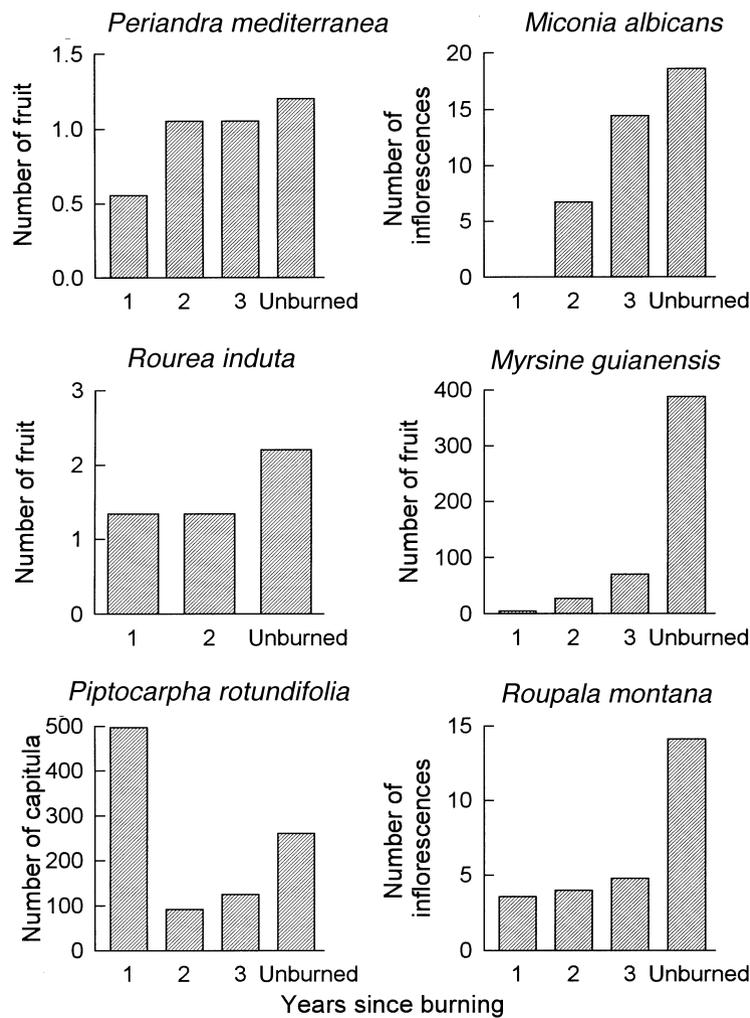
Fig. 4. The overall effect of burning on sexual reproduction. These values show the changes in fecundity resulting from the combined effects of fire on individual size and on size-specific reproductive output. The effects of fire on individual size were used to adjust the size-specific rates of reproductive output, to compare individuals of the same pre-burn size.

reproduce under current fire regimes of biennial to triennial burns, but *Miconia* is not. Indeed, this species is virtually absent in frequently burned sites and is abundant in adjacent protected sites (Moreira 1992), even though adults are able to resprout vigorously. For this species the negative effect of fire on reproduction has also been observed in savannas of Belize (Miyanishi & Kellman 1986) and the Amazon (Sanaiotti & Magnusson 1995).

For the trees *Myrsine* and *Roupala*, estimates of time required for reproduction are probably overly optimistic. Individuals reproducing in the first 3 years after burning were invariably individuals that were not top-killed. Resprouting individuals did not have sufficient time to reach sexual reproductive size during this time. Under frequent burning, the number of sexually reproductive individuals will gradually decline, as each successive fire will top-kill a fraction of the remaining large individuals. Eventually, most or all of the population may be maintained in a diminutive state, never able to reach sexual reproductive size.

Likewise, seedlings, although able to survive fire, will be unable to reach reproductive size under frequent burning. It is likely that tree species incapable of vegetative reproduction would be unable to persist under continued frequent burning.

Although burning tended to reduce sexual reproductive success, fire stimulated vegetative reproduction by increasing the production of root suckers. This effect was clear for three of the four study species capable of producing root suckers – *Rourea*, *Myrsine* and *Roupala*. For the fourth species, *Piptocarpha*, the sample size was too small to test conclusively for burning effects. Similar responses to fire have been documented in species of other regions (Barnes 1966; Lacey 1974; Farrell & Ashton 1978; Abrahamson 1980; Lamont 1988; Lacey & Johnston 1990; Matlack, Gibson & Good 1993). The formation of root buds can be stimulated by the reduction in auxin content resulting from the loss of aerial biomass (Peterson 1975), by increased soil temperature (Miani & Horton 1966; Peterson 1975) resulting from greater insolation following fire, or by
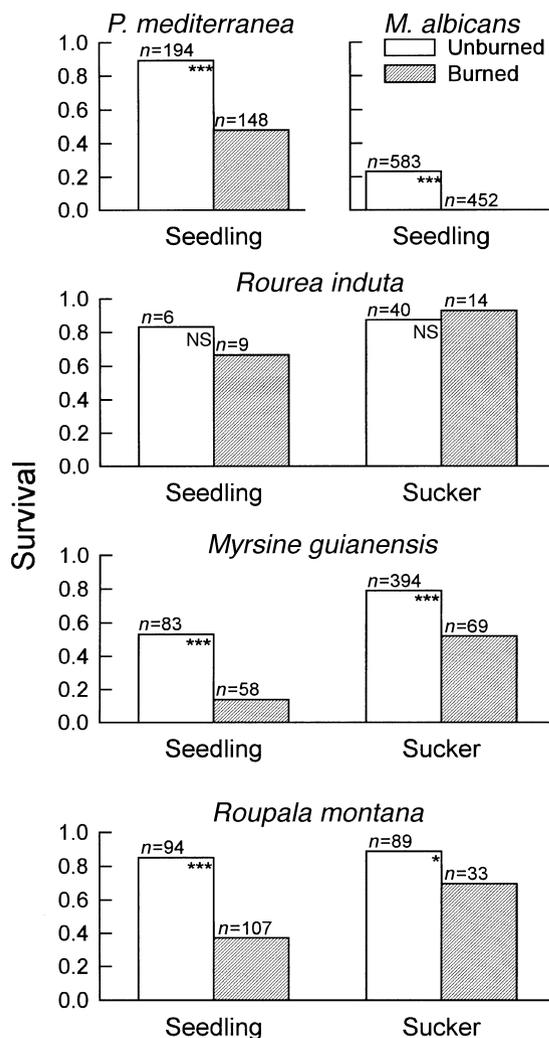
Fig. 5. Effect of burning on survivorship of seedlings and suckers. Survival was evaluated for the 1-year period beginning at the start of the first dry season. Differences in survival between the burned and unburned treatments are indicated by $*P \leqslant 0.05$, $**P \leqslant 0.01$, $***P \leqslant 0.005$.

relative to seedlings reinforces the importance of vegetative reproduction under frequent burning. Because they are more likely to survive burning and reach sexual maturity earlier, a sucker will contribute more to future population growth than a seedling. Since root suckers are produced shortly after burning and are quite tolerant of fire, vegetative reproduction may allow a species to reproduce even if the time between fires is too short for sexual reproduction to succeed. A clone may be able to expand as a population of reduced stems until a prolonged fire-free interval permits them to reach adult size. Evidence of this is particularly clear for *Myrsine*. Near the study site a patch of this species covers an area of several hectares. Prior to fire protection the site was occupied by campo sujo, or open shrub savanna (B. Dias, personal communication). After 20 years of fire protection the site is now quite dense savanna, almost completely dominated by adults of *Myrsine*. Examination of this patch revealed that it comprised entirely males, indicating that it was probably derived from one or several clones. Prior to fire protection the site was undoubtedly occupied by a population of reduced stems. These stems, upon release from burning, developed into a stand of trees. Similar behaviour has been observed in several rhizomatous eucalypti in the northern Australian savannas (Lacey 1974).

The ability of some woody plants to spread clonally may play an important role in the expansion of woody cover in grass-dominated sites and degraded sites. In the cerrado and other savannas, seedling establishment is facilitated by woody cover (Kellman & Miyanishi 1982; Kellman 1985; Callaway 1992; Hoffmann 1996). The lateral expansion of clones into treeless patches is expected to speed the establishment of other species. A similar scenario has been observed in the tallgrass prairie of North America, where clonal expansion of the shrub *Rhus copallina* plays an important role in the expansion of forest into prairie by improving conditions for tree seedling establishment (Petranka & McPherson 1979).

The large post-burn flush of root suckers is analogous to the establishment of large cohorts of seedlings observed in many fire-prone ecosystems (Bond, Vlok & Viviers 1984; Wellington 1989; Keeley 1991). Post-fire seedling establishment, which does not appear to be common in cerrado plants, requires some mechanism to protect seeds from fire. Some cerrado species have fruits that protect seeds from burning (Coutinho

physical damage to the root (Rizzini & Heringer 1962; Peterson 1975). In the present study, direct damage to the root apparently caused some of the root buds to form. Some suckers originated from shallow roots that had been damaged by fire, but this accounted for relatively few suckers. Only the most shallow roots are in danger of fire damage, since soil temperatures at a depth of 1 cm have not been found to exceed 55 °C during burns (Coutinho 1978; Miranda *et al*. 1993).

The larger size and greater fire tolerance of suckers

Table 2. Comparison of seedling and sucker stem diameters

Species	Seedling stem diameter (mm) $\pm$ SE	Sucker stem diameter (mm) $\pm$ SE	Student's t	P
Rourea induta	0·61 $\pm$ 0·02	2·43 $\pm$ 0·43	4·23	<0·0001
Myrsine guianensis	0·81 $\pm$ 0·01	1·72 $\pm$ 0·04	22·75	<0·0001
Roupala montana	0·95 $\pm$ 0·01	1·88 $\pm$ 0·11	8·42	<0·0001

Table 3. Summary of the reproductive responses of the study species to burning

Species	Growth form	Maximum height (approx.)	Reproduces vegetatively?	Effect of burning on seed production	Survival of burned seedlings
Periandra mediterranea	Subshrub	2 m	No	Negative	Intermediate
Miconia albicans	Shrub	3 m	No	Negative	None
Rourea induta	Shrub	3 m	Yes	Negative	High
Myrsine guianensis	Tree	9 m	Yes	Negative	Low
Piptocarpha rotundifolia	Tree	6 m	Yes	Positive	?
Roupala montana	Tree	9 m	Yes	Negative	Intermediate

1977a; Landim & Hay 1996) but most species, including those studied here, lack such structures. However, the possibility that some seed survives in a buried seed bank was not explored here. Also, in low-intensity burns, seeds above the scorch height may survive but this was not observed in the study plots. Although some seeds may fortuitously survive burning, the fraction is likely to be small.

The scarcity of adaptations to protect seeds, such as serotinous fruits, might be explained by the poor conditions for seedling establishment that occur during the first year after burning (Hoffmann 1996). In the savanna, where plant and litter cover ameliorate conditions for seedling establishment (Kellman & Miyanishi 1982; Kellman 1985; Callaway 1992), removal of cover by burning is detrimental to germinating seedlings. Thus, there may have been little selective pressure for adaptations that ensure seed availability immediately after burning.

In conclusion, fire had substantial effects on all stages of sexual and vegetative reproduction examined here. Although conversion to agriculture is the most serious threat to cerrado ecosystems (Klink, Moreira & Solbrig 1993), fire continues to be the most frequently used management tool in the cerrado (Pivello & Coutinho 1996). Under the annual to triennial burning typical of current fire regimes in the cerrado, success is dependent upon the ability to reproduce vegetatively, the ability to produce seeds shortly after fire, and the ability of offspring to survive burning. The six study species varied greatly with respect to all three of these variables (Table 3), indicating large interspecific variability in fire sensitivity. Although these represent only a fraction of the diverse woody plant flora of the cerrado, and although the effect of fire on reproduction offers an incomplete view of how a population responds to burning, we can surmise that the cerrado is undergoing large-scale shifts in community composition. In particular, species that are unable to reproduce vegetatively are likely to be at a greater disadvantage under frequent burning.

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Appendix

MAXIMUM LIKELIHOOD ESTIMATION OF ROOT SUCKER PRODUCTION

Ribbens, Silander & Pacala (1994) developed a method to estimate the relationship between stem diameter and the number of offspring produced, even when it is not possible to determine which adult produced a particular offspring. I modified this method, simplifying much of the spatial component of the analysis in order to reduce the number of parameters to be estimated.

I assume that the relationship between stem diameter (d) and the number of suckers produced (S) follows some allometric relationship:

$$S = \alpha \cdot d^{\beta} \qquad \text{eqn 1}$$

where α and β are parameters that need to be estimated. The mean density (D) of suckers produced within a population of adults will be:

$$D = \frac{\sum_{i=1}^{n} (\alpha \cdot d_i^{\beta})}{A_a} \qquad \text{eqn 2}$$

where A_a is the area of a representative sample of the adult population, and n is the number of trees in the area. By sampling a population, one can obtain empirical values for D, A_a and the d_i in equation 2, leaving only α and β unknown. By sampling numerous populations it is possible to estimate α and β. Here a maximum likelihood estimator was used to find the values of α and β that best predict the observed densities of suckers in the study plots.

If the density of suckers within a plot is estimated by sampling a subplot of area A_s, the predicted number of suckers in the subplot will be $A_s \cdot D$. The actual number will be distributed according to a Poisson distribution, assuming that suckers are produced independently of each other.

For the maximum likelihood method, parameter values are found that maximize the log likelihood (Rice 1988), which is:

$$L = \sum_{j=1}^{m} \left(-Pred_j + Obs_j \cdot \ln (Pred_j) - \ln (Obs_j!) \right) \qquad \text{eqn 3}$$

$Pred_j$ and Obs_j are the predicted and observed numbers of suckers in subplot j, and m is the number of plots sampled. By combining equation 2 with equation 3, the log likelihood is:

$$L = \sum_{j=1}^{m} \left(-\frac{A_s}{A_a} \sum_{i=1}^{m} \alpha \cdot d_i^{\beta} + Obs_j \right.$$

$$\left. \cdot \ln \left(-\frac{A_s}{A_a} \sum_{i=1}^{m} \alpha \cdot d_i^{\beta} \right) - \ln (Obs_j!) \right) \qquad \text{eqn 4}$$

In equation 3, only L, α and β are unknown. Using a maximization algorithm, it is possible to find the values of α and β that maximize L. These values are the maximum likelihood estimates of α and β. To find the values of α and β that maximize L, I used a Turbo Pascal program utilizing the downhill simplex method (Press *et al.* 1989). Copies of the program are available upon request.

In the present study, I used a 15×25-m plot for sampling the adult population, and counted suckers within a 5×15-m subplot, so $A_a = 375$ and $A_s = 75$. The subplots were centred within the plots in order to reduce possible edge effects.

MONTE CARLO SIMULATIONS

Monte Carlo simulations were used to confirm that the above maximum likelihood estimator gives unbiased estimates of sucker production. In each simulation, 22 plots were generated, each with a random number of adults. Each adult was randomly located within the plot and its stem diameter was randomly generated from an exponential distribution. The number of suckers produced per individual was generated from a Poisson distribution, with the expected number of suckers (S) arbitrarily chosen to be the allometric function of stem diameter:

$$\lambda = 0.003 d^{1.8} \qquad \text{eqn 5}$$

For each sucker, distance from the parent was randomly generated from an exponential distribution and the angular direction from the adult was randomly generated.

The maximum likelihood estimator was then applied to the generated data. The parameter β was fixed at its true value and the parameter α was estimated. This was performed for 5000 simulations to determine the mean and variance of the estimates.

The Monte Carlo simulations confirmed that the maximum likelihood estimator provides reliable estimates of sucker production. The 5000 simulations resulted in a mean estimate $\hat{\beta} = 0.002996 \pm 0.00034$ (mean $\pm$ SD). Thus, the estimated value did not differ significantly from the true value of 0.003 ($z = 0.81$, $P = 0.79$).