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REVIEW

Effects of prescribed fires on the survival and release of seeds of *Kielmeyera coriacea* (Spr.) Mart. (Clusiaceae) in savannas of Central Brazil

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Effects of prescribed fires on survival and release of seeds of the woody species *Kielmeyera coriacea* (Clusiaceae) were investigated in two plots of cerrado *sensu stricto*, a savanna vegetation of Central Brazil. The first plot was burnt in June, at the beginning of the dry season, and the second in August, in the middle of the dry season. Seed survival was measured after fire in both areas and related to internal and external fruit temperatures measured during the June fire. The proportion of open fruits per individual of *K. coriacea* was also assessed at two-week intervals. Maximum external temperatures during fire (393 to 734^{o}C) were strongly reduced inside the fruits (61 to 63^{o}C). Before the June fire, the majority of the fruits were closed in both plots. Most fruits in the June plot opened within two weeks following the burning while, in the same period, most fruits remained closed in the August plot. Fifteen days after the prescribed fire in the August plot most fruits opened, as observed in the June plot. No germination was observed in seeds from closed fruits collected before the fire, while those from fruits that were closed during the burning showed a high mean germination rate (June = 79 ± 12%; August = 69 ± 14%). The results indicate that fruits of *K. coriacea* are good insulators for seeds during fires and that seed release is anticipated independently of the burning season.
Key words: Cerrado, fire season, fruit temperature, germination, seed release

Efeito de queimadas prescritas na sobrevivência e dispersão de sementes de *Kielmeyera coriacea* (Spr.) Mart. (Clusiaceae) em áreas de cerrado *sensu stricto*: Os efeitos de queimadas prescritas na sobrevivência e na dispersão de sementes de *Kielmeyera coriacea* (Clusiaceae) foram investigados em duas parcelas de cerrado *sensu stricto*, uma queimada no início da estação seca (junho) e outra, em agosto, meio da estação seca. A sobrevivência das sementes após as queimadas foi relacionada às temperaturas externa e interna dos frutos medidas durante a queimada de junho. A proporção de frutos abertos por indivíduos de *K. coriacea* foi observada quinzenalmente. As temperaturas externas máximas durante a passagem do fogo (393 a 734^{o}C) foram fortemente reduzidas dentro dos frutos (61 a 63^{o}C). Nas duas parcelas, a maior parte dos frutos estava fechada antes da queimada realizada em junho. Cerca de 60% dos frutos observados na parcela queimada em junho abriram nas duas semanas após a queimada sendo que, no mesmo período, a maior parte dos frutos na parcela a ser queimada em agosto permaneceu fechada. Da mesma forma, nas duas semanas seguintes à queimada realizada em agosto, foi observada a abertura da maioria dos frutos. Nenhuma semente dos frutos coletados antes das queimadas germinou. Entretanto, foi alta a germinação das sementes coletadas dos frutos que estavam fechados durante as queimadas (junho = 79 ± 12%; agosto = 69 ± 14%). Os resultados indicam que os frutos de *K. coriacea* oferecem boa proteção para as sementes durante as queimadas e que, independentemente da época da queima, a dispersão das sementes é antecipada pela passagem do fogo.
Palavras-chave: Cerrado, fogo, temperatura do fruto, germinação, dispersão de sementes

INTRODUCTION

Fire is considered to be an important ecological feature in several plant communities creating opportunities for establishment, growth and reproduction of many species, and restraining the less resistant ones (Whelan, 1995; Cirne and Scarano, 2001; Cirne et al., 2003). In areas with high susceptibility and recurrence of burning, some fire-related characteristics tend to be selected, and the success of each is determined by intrinsic (anatomical, morphological, physiological and growth patterns) and extrinsic factors such as climate and fire regime (Lamont et al., 1991; Tyler, 1995; Hanley and Fenner, 1997). Studies concerning the components of the fire regime, such as season of burning, are particularly important for understanding patterns of plant distribution and different regeneration strategies, especially in areas with climatic seasonality (Bond, 1984; Cowling and Lamont, 1987; Williams et al., 2004).

At the individual level, the survival of a plant will depend on the amplitude and duration of the temperatures during fire, since an increase in temperature will correspond to a decrease in the period of exposure required to promote injury in living tissues (Wright and Bailey, 1982). In the case of seeds, thermal insulation can be improved if they are buried in the soil and/or have a hard coat (Lamont and Baker, 1988; Auld and O'Connell, 1991; Eriksson et al., 2003), by fruit location in the plant (Judd and Ashton, 1991; Judd, 1993), or by a thick fruit wall or high moisture content of fruits (Judd, 1994; Bradstock et al., 1994; Mercer et al., 1994; Bell and Williams, 1998). Few studies report direct field measurements quantifying the reduction of temperatures by fruits during fires (Judd, 1993; Bradstock et al., 1994).

For many species, fruit opening may be anticipated by fire, as has been reported for some wind-dispersed plants of the Cerrado (Coutinho, 1977), a savanna vegetation in Central Brazil. Natural or human initiated fires have been a feature of this Biome for more than 32,000 years (Salgado-Labouriau and Ferraz-Vicentini, 1994). The alteration in species composition and vegetation structure as a consequence of a high fire frequency on the Cerrado vegetation (Medeiros and Miranda, 2005, 2008), together with the replacement of the native vegetation by crops and pastures, has included the Cerrado in the list of 25 world biodiversity "hotspots" (Myers et al., 2000; Cardoso and Bates, 2002). Research on the effects of different fire regimes, especially the burning season, on the reproduction of Cerrado vegetation is important for its conservation.

This study examined the importance of the fruits of *Kielmeyera coriacea* (Clusiaceae) as thermal insulators for seeds during the fire in a cerrado *sensu stricto* with a dense cover of shrubs and trees and a rich grass understory, the most common Cerrado phytophysiognomy (Eiten, 1972). The effects of time of fire (beginning and middle of the dry season) on seed release were analyzed. The following questions were addressed: 1) Are *K. coriacea* fruits good insulators for seeds during fires? 2) Are seeds in open fruits and those protected in closed fruits capable of surviving a fire? 3) Does the fire season alter the natural phenological patterns of *K. coriacea* fruit opening and seed release?

MATERIAL AND METHODS

The study was carried out in the Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística, 35 km south of Brasília (15°56'41"S, 47°53'7"W), Brazil. The Reserve has an area of 1360 ha at an altitude of 1100 m, and the mean annual precipitation is 1353 mm.

Two contiguous plots (10 ha each, 200 m x 500 m) of cerrado *sensu stricto* were used in the study. Both plots had been protected from fire for 18 years until 1992. Since 1992, one of the plot has been burned biennially in June (beginning of the dry season) and the other, in August (middle of the dry season). The biennial fire frequency has been applied to simulate the most common fire frequency in the region (Coutinho, 1982).

The native species, *Kielmeyera coriacea* can be found in most Cerrado physiognomic forms, and is one of the few woody species which dominates the more open physiognomies of this biome (Aoki and Santos, 1982; Ribeiro et al., 1985). Some individuals may reach up to 8 m in height (Almeida et al., 1998), and its phenological patterns are markedly seasonal: complete fall of leaves during one or two months of the dry season and flower production from September to January, beginning to middle of the rainy season. The fruits are dehiscent and large, 16 cm length by 5 cm width, with an average of 63 seeds per fruit. After a long period of maturation, lasting most of the subsequent dry season, the fruits are totally open and the seeds can be easily detached and dispersed by wind in synchrony with the beginning of the rains (Ribeiro et al., 1985; Oliveira and Silva, 1993; Landim and Hay, 1996).

The role of *K. coriacea* fruits in protecting the seeds during fires was investigated, during the prescribed fire of June 2000, by measuring external temperature at the fruit surface and the internal temperature near the seeds. Seed position inside the fruits was estimated from laboratory observations of seed position in relation to fruit size. Temperatures in three fruits were measured with thermocouples type k (30 swg), recorded at one second interval and stored automatically in a data logger (21X, Campbell Scientific, Inc., E.U.A.). In both plots, the mean fruit height was 2.1 ± 0.8 m, and the sampled fruits were located between 2.0 m and 2.3 m in height.

Seed survival in both areas was analyzed through germinability of seeds collected in fruits opening after the prescribed fires. Immediately after the June and August burns, 20 to 25 closed fruits, from different individual plants, were covered with cotton net bags to ensure no loss of seeds after fruit opening. Seeds from 10 fruits that opened in the week following the fires were collected for germination test. Ten samples, with 10 seeds each, were used for each plot. The seeds were placed in Petri dishes with wet filter paper to germinate at room temperature and light conditions. Newly germinated seeds were counted daily. The geotropic curvature of the radicle was used as the germination criterion. The significance of differences between the germination rates of seeds collected in fruits opened after the June and August fires was tested (t test; Zar, 1996), after arcsine transformation. The same methods and sample size were used to obtain the germination rate of seeds from closed fruits collected immediately before the June and August fires, and for seeds collected, immediately after the fires, from fruits that were open in the plots. Closed fruits were opened manually to collect the seeds and, to avoid any effect of storage, all germination tests were carried out immediately after seed collection.

To analyze the effect of burning and fire season on the time of fruit opening and seed release, 15 individuals, with a minimum of three fruits each, were tagged in each plot. Total number of fruits in the tagged trees was 114 in the June plot and 125 in the August plot. The proportion of open fruits was observed at two-week intervals, before and after the fires. The significance of the differences between the values observed in consecutive weeks was tested by the Mann-Whitney test (α = 0.05). The proportion of open fruits in the August plot was used as control (i.e. without fire) for the plot burnt in June.

The relative water content (water mass/dry mass) was determined for 10 closed fruits collected one hour before the prescribed fire in June and for another 10 closed fruits collected 15 days after the fire. Fruit fresh mass was measured in the field and the dry mass was obtained after drying the fruits at 80°C until constant mass. Ten closed fruits collected in the June plot, 15 days after the fire, were used to estimate the relative water content for the fruits to open. Relative water content was also measured for 10 fruits collected one hour before the fire in the August plot. The significance of differences between the relative water content was tested (t test; Zar, 1996).

RESULTS

The increase in temperature was 19 times greater at fruit surface than inside the fruit. Maximal external fruit temperatures during the fire ranged from 393°C to 734°C (Figure 1a) with a mean value ± SD of 597 ± 180°C. Internal fruit temperatures (Figure 1b) were in the range of 61°C to 63°C with a mean value of 62 ± 1°C. At the fruit surface, temperatures greater than 60°C were observed for 106 ± 19 s, and inside the fruits for 99 ± 12 s (Figure 2).

Seeds collected from fruits that were open before the fires did not germinate in laboratory tests. For seeds collected from fruits that opened after the fire, the germinability was high for both plots: 79 ± 12 % and 69 ± 14 % for fruits in the plots burnt in June and August, respectively. Germination rate was not significantly different ($t = 1.725$; $p>0.05$) between plots. Seeds collected from closed fruits before the prescribed fires of June and August did not germinate.

Before the June fire, the median value of open fruits in the tagged individuals was zero. Two weeks after fire, the median value increased to 66.6% in the June plot (Figure 3) and no alteration was observed at this time in the percentage of open fruits in the August plot. The difference in percentage of open fruits between plots was significant ($p<0.05$) until two weeks after the prescribed fire of August. After the August fire, an increase in the percentage of open fruits was observed in this plot, as it

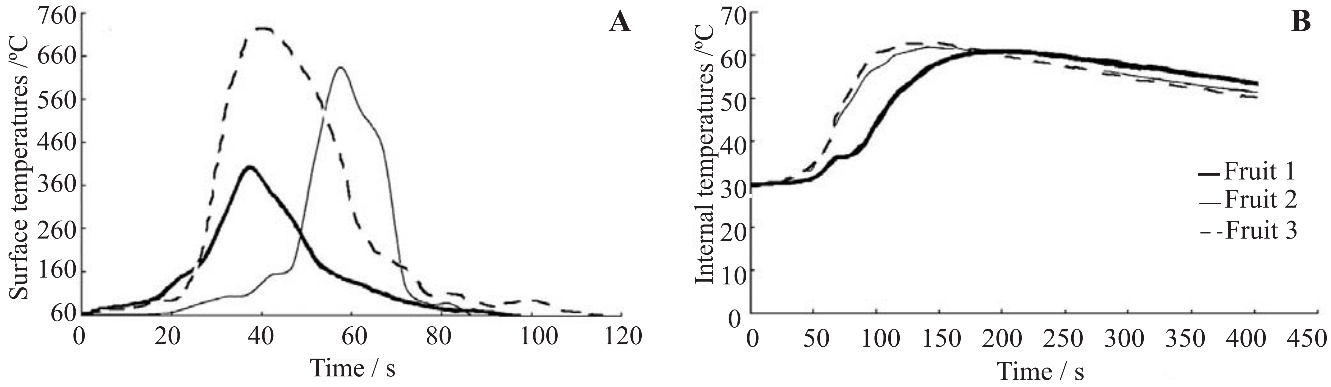

Figure 1. External (a) and internal (b) temperatures for three fruits of *Kielmeyera coriacea* during a prescribed fire in June of 2000 in a cerrado *sensu stricto* area at the Reserva Ecológica do IBGE, Brasília, Brazil.

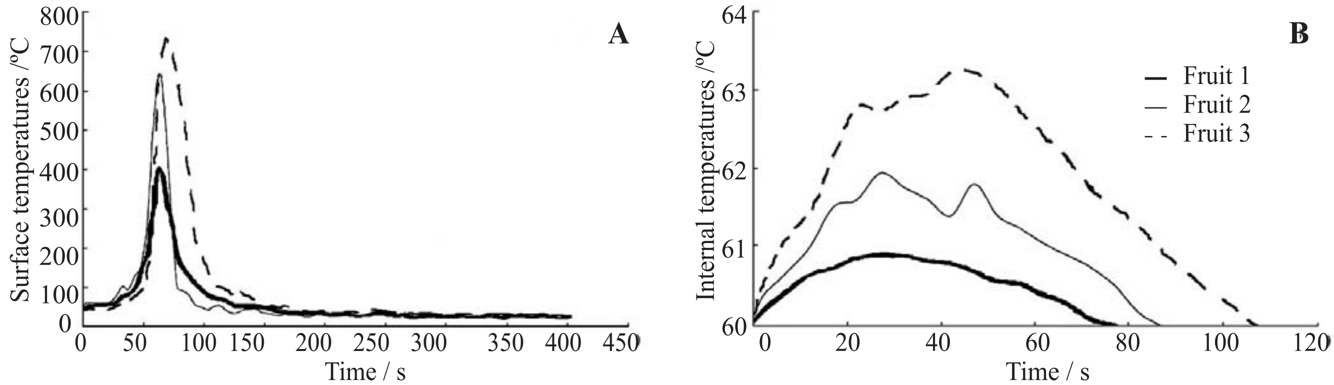

Figure 2. Duration of external (a) and internal (b) temperatures greater than 60ºC for three fruits of *Kielmeyera coriacea* during a prescribed fire in June of 2000 in a cerrado *sensu stricto* area at the Reserva Ecológica do IBGE, Brasília, Brazil.

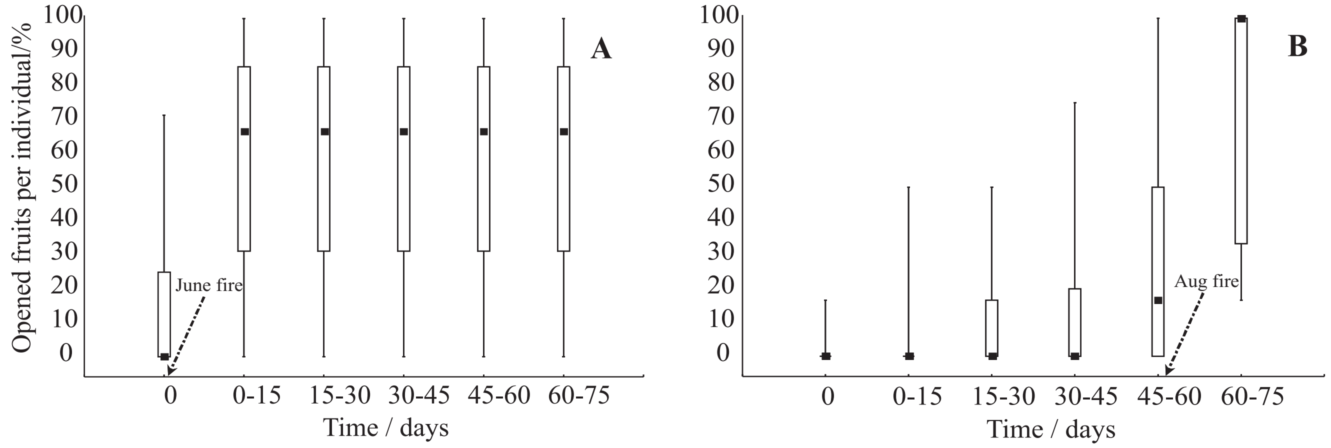

Figure 3. Median number of open fruits per individual of *Kielmeyera coriacea* in areas of cerrado *sensu stricto* (closed squares) submitted to prescribed biennial burnings at the beginning - June (a) and at middle - August (b) of dry season. Significant differences (n = 15; $p<0.05$) in consecutive samples in each plot were observed only after the respective burning. Bars = inferior (25%) and superior (75%) quartiles; whiskers = maximum and minimum values.

was observed after the prescribed fire of June. The percentage of fruits that did not open until the end of the subsequent rainy season was 41.2% and 34.4% in the plots burnt in June and August, respectively.

For closed fruits collected in the June plot, on the day of the fire, the relative water content (RWC) was 528.8 ± 90.9%, reducing to 422.0 ± 72.5% two weeks later. Before the fire in the August plot RWC for the closed fruits was 403.3 ± 25.0%. In the laboratory, fruits opened when RWC reached 333.1 ± 59.6%. The differences between RWC of fruits collected before and 15 days after the June fire were significant ($t = 2.9026$; $p<0.05$) but no difference was observed between fruits collected after the June fire and those collected before the August fire ($t = 0.7748$; $p>0.05$).

DISCUSSION

During the fire, surface temperatures as high as 734 °C were measured for fruits of *Kielmeyera coriacea*, with maximum internal temperatures of 63 °C. This value is lower than the lethal temperature of 70 °C reported by Mercer et al. (1994) for species with seeds without a hard coat such as *K. coriacea*. The high germination rate observed for the seeds collected in fruits that opened after the June and August fires is a measure of the efficiency of *K. coriacea* fruits in attenuating the high external temperatures. The role of fruit in protecting seeds during fires is emphasized by the absence of viable seeds among those collected from open fruits. Even for seeds with hard coats and dependent on fire to break dormancy, the direct exposure to high temperatures can be lethal to embryos (Hanley et al., 2001; Danthu et al., 2003).

The residence time for internal fruit temperatures greater than 60°C was not long enough to cause damage to the seeds. Internal temperatures may be related to the short residence time of high external fruit temperature during fires, fruit characteristics and moisture content (Judd and Ashton, 1991; Judd, 1993, 1994; Mercer et al., 1994). Bradstock et al. (1994) report that *Hakea dactiloydes* seeds may be able to withstand exposures of up to 300 s at 60°C. Although the insulating capacity of fruits may be associated mainly to the fruit wall thickness (Judd, 1994), the high water content associated with the large size of *K. coriacea* fruits may also explain the values of internal fruit temperatures given that the evaporation of moisture prevents internal temperature from rising above 100°C until the fruit tissue has dried (Judd, 1993, 1994; Mercer et al., 1994).

More than 70% of the seeds from fruits that opened after the fires in the June and August plots germinated, but none from the closed fruits that were collected just before the fires, suggesting that the early dry season fire coincided with seed maturation (Figure 3). Fruit opening after the burnings may be a consequence of the death of branches caused by cambium temperatures greater than 70°C (Cirne, 2002). This will interrupt sap flow to the fruits, which may be the signal that initiates the final phase of seed development (pre-abscission), when they lose water and dry maturation occurs (Hay and Probert, 1995; Baskin and Baskin, 2001). Despite the effects of high temperatures, high rates of germination can also be achieved by inactivation of inhibitors of germination and/or by the release of chemical compounds necessary for this process (Bell and Williams, 1998; Whelan and Brown, 1998). However, for *K. coriacea* fire does not represent an essential factor for seed germination. The germination rates of *K. coriacea* seeds from fruits that were not exposed to fire reported by Oliveira and Silva (1993) were similar to those observed in the present study.

In the Cerrado, fruit opening and seed release of *K. coriacea* occur throughout the dry season, with a peak at the end of the season (Ribeiro et al., 1985, Oliveira and Silva, 1993), when wind conditions and the low relative humidity favor wind dispersal (Gottsberger and Silberbauer-Gottsberger, 1983). There is a synchronic release of seeds near the beginning of the rainy season, when the chances of germination are higher (Oliveira and Silva, 1993). In the present study, fruit opening occurred earlier after the June fire, with most of the fruits opening in the first two weeks after the fire. In the August plot, which represented a control treatment (without fire) for the June fire, most of the fruits remained closed during the same period (Figure 3). After the August fire, an intense peak of fruit opening also occurred in the two weeks following the fire, similarly to the pattern observed after the June fire. In both plots, seed release was anticipated by the fire independently of the timing of burning. Nevertheless, for the August plot, the lack of an unburned control prevented any clear distinction of the effects of fire from the phenological patterns of *K. coriacea* in fruit opening.

Fruit opening after fire may occur as a function of exposure to the high temperatures that kill living tissues resulting in desiccation and subsequent rending of the fruit structure (Gill, 1976; Bradstock and Myerscough, 1981; Richardson et al., 1987; Lamont, 1991; Judd, 1994). A reduction in the relative water content (RWC) of closed fruits of *K. coriacea* was observed when comparing the values obtained before the June fire and those measured 15 days after the fire. The reduction in RWC of closed fruits collected before the fires in the June and August plots represent the natural pattern during the dry season, following the reduction of the air relative humidity. Although RWC of closed fruits measured after the fires is greater than the relative water content measured for fruit opening, the differences between pre and post fire RWC of fruits collected in the June plot, and the similarity between the RWC of fruits collected 15 days after the June fire and those collected before the August fire may indicate that the fire is accelerating fruit drying and anticipating the release of the seeds.

The adaptive significance of synchronic seed release after fire, as observed in the June and August plots, can be explained by the exploitation of favorable conditions for germination and establishment frequently occurring after fires (Coutinho, 1980; Whelan, 1985; Lamont et al., 1991; Bradstock et al., 1994). Also, wind dispersed seeds, such as in *K. coriacea*, can spread over greater distances as a consequence of the removal of the plant cover by fire, as observed by Coutinho (1977) for other woody species of the Cerrado.

Although fire may stimulate the release of seeds, it can also result in the mortality of a large proportion of seeds if the phenological patterns of the species results in seed release prior to late dry season fire. For *K. coriacea*, the opening of fruits before the fire (13.2% of total in the June and 22.4% in the August plots – Figure 3) will result in death of seeds in the open fruits. Also, 41.2% of the fruits in the June plot and 34.4% in the August plot did not open after the fires, which represents an additional loss of seeds. A large proportion of fruits of *K. coriacea* failing to open after a fire was also observed by Landim and Hay (1996). Considering fruits that were open before the fires and the ones that did not open afterwards, the estimated loss of seeds was 54.2% in the June plot and 56.8 % in the August plot. Also, the success of seed germination is frequently maximized if it occurs quickly after seed release (Bond, 1984; Cowling and Lamont, 1987; Whelan and Tait, 1995). Thus, the synchronic fruit opening at the beginning or the middle of the dry season represents further risks of seed death by increasing exposure time of the seed at the soil surface, since the rainy season is expected to start approximately four months after the June fire.

CONCLUSIONS

The questions addressed in this work were positively answered: *K. coriacea* fruits offer good thermal insulation for seeds during Cerrado fires; the duration of internal fruit temperatures above 60°C is not long enough to damage the seeds inside closed fruits exposed to the flames or to the hot air flow during fires; seeds from fruits that open after exposure to fire showed high germination rates, and seed release is anticipated independently of time of burning. However, the damage of viable seeds in fruits that are already open before the fires and the large number of fruits that do not open after the fires represent a considerable loss of the year's seed production.

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