

Effects of fire on germination of *Pterocarpus angolensis*

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Abstract

Pterocarpus angolensis (Fabaceae) is a leguminous tree species of the miombo region of sub-Saharan Africa that is highly prized for its wood value. We use both experimental exposure to fire, as well as classification of field burned seeds, to predict germination rates in seeds from both husked and unhusked fruits. We find that seed germination and seed persistence in unhusked fruits are maximized by moderate exposure to fire. Germinating seeds had heavier fruit and seeds than those that did not. Finally, seeds without husks persisted in the soil yet continued to germinate even after 18 months in wet soil, indicating potentially long soil longevity. Using these results, we support an intermediate fire exposure model wherein repeated moderate exposure to fire enhances the capability of seeds to emerge from fruits. Seeds from unburned and unhusked fruits were never observed to germinate and had poorer soil longevity than those exposed to moderate fire. Similarly, extreme exposure to fire resulted in poor seed germination rates, often as a consequence of direct fire mortality of seeds. We suggest that early burning resulting in cool fires may augment germination and recruitment in wild populations.

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1. Introduction

Leguminous trees of savanna woodlands produce hard seeds with high dormancy that is broken by physical rupturing of the seed coat (Walters et al., 2004). Fire has been suggested as an important germination stimulant that acts by rupturing the protective fruit and allowing entry of water thereby triggering the germination process (Sabiiti and Wein, 1987; but see Saharjo and Watanabe, 1997). At high temperatures, however, fire can cause seed mortality (Auld and O'Connell, 1991). The purpose of this study was to investigate the germination response of a tropical savanna timber species, *Pterocarpus angolensis*, to fire. *P. angolensis*, a leguminous tree species from the eastern, central and southern regions of Africa, is one of the most valuable timber species within its distribution. This species is widely utilized for building, furniture, veneer, carving and general-purpose timber (Monela et al., 1993) as well as for traditional medicine (Watt and Breyer-Brandwijk, 1962; Palgrave, 1981; Ndamba et al., 1994; Nyanzema et al., 1994; Van der Reit et al., 1998). Populations of *P. angolensis*

have dramatically declined due to selective harvest throughout their range (Shackleton, 2002; Caro et al., 2005).

A slow growing tree, *P. angolensis* matures at somewhere between 15 and 20 years (Boaler, 1966). Mature trees produce up to several hundred large wind-dispersed fruits with a stiff circular, membranous wing and dense, bristly center that contains one and sometimes two seeds. Fruits remain indehiscent at maturity, and require physical abrasion or other mechanisms to open the fruit and allow seeds to imbibe and germination to proceed. Seeds typically germinate from within opened fruits (Boaler, 1966).

It has been observed that successful germination of *P. angolensis* seeds is a relatively rare event. According to Boaler (1966) only 2% of seeds produced germinate under natural conditions. Of the seedlings produced, half die during their first year. Luckoff (1969) recorded about 10,000 healthy seeds/ha but very few seedlings. Several studies have attempted to establish reasons for this lack of germination. Van Daalen (1991) showed that seeds collected from trees were more viable than those collected from the ground and that fungal infections and cool temperatures did not affect the germination of seeds. Caro et al. (2005) showed that short grass and reduced parent canopy cover was associated with higher seedling density, indicating that light and precipitation might play a role in germination and seedling

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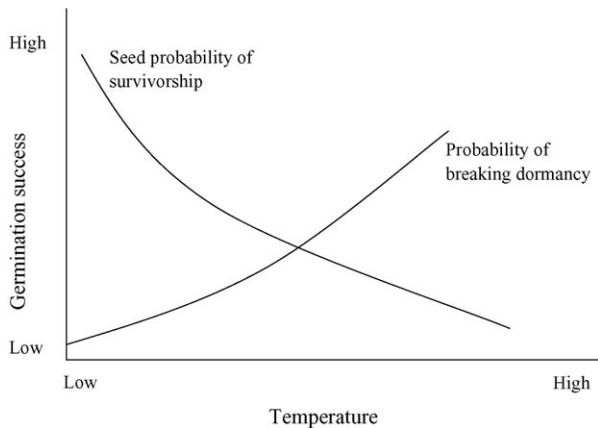


Fig. 1. A conceptual framework for our hypothesized effects of fire on *Pterocarpus angolensis* seed germination success. Our hypothesis predicts that the probability of seed survivorship decreases with exposure to fire, while the probability of a seed being able to break out of the hard woody fruit casing increases with scarification through fire. Thus, our hypothesis suggests a maximum recruitment potential at an intermediate exposure to fire under field conditions.

survival. Finally, Van Daalen (1991) also showed that high temperatures can kill seeds. Nevertheless, the robust fruit of *P. angolensis* inhibits emergence and exposure to fire may be required to break open fruits in order to allow emergence.

The focus of this research was to study the possible positive and negative aspects of exposure to fire in the germination of *P. angolensis*. Specifically, we predict that germination potential peaks with intermediate exposure to fire (Fig. 1). Secondly, we hypothesize that fruit and seed size affect seedling survival sensitivity to fire. Thus, we expect this intermediate exposure to fire to vary with fruit and seed size. We investigated the role of fire on fruits and seeds collected from the Katavi ecosystem in western Tanzania (Caro, 1999). We chose this region because of observations of poor tree recruitment both within the national park as well in selectively harvested adjacent areas (Schwartz et al., 2001; Schwartz and Caro, 2003; Caro et al., 2005).

2. Methods

We conducted a series of experiments using field collected fruits that had or had not been exposed to fire at the time of collection from the ground. We classified field burned fruits, as described below. Unburned fruits were exposed to varying lengths of fire treatment in the laboratory. Following treatments, seed germination rates were recorded for both husked fruits as well as unhusked fruits. Experiments with husked seeds focused on understanding the relationship between fire exposure levels and direct seedling mortality by assessing germination rates. Experiments with unhusked seeds focused on understanding the potential positive effects of fire exposure to germination potential.

2.1. Husked seed preparation

We investigated how seed germination is affected by burn duration, seed weight, and fruit weight. By design, half of our

field collected fruits ($n = 320$) had already experienced at least one fire in the field. These natural fire fruits were visually inspected in the laboratory and classified according to their degree of burning into one of five categories. Fruits were then weighed and cracked open, seeds extracted and weighed. Eighty-six fruits were either barren (empty fruit) or contained seeds that were shriveled or charred by intense fire in the field. A few (~ 10) were discarded because they were destroyed by researchers while opening the fruit. Seventy-four seeds of healthy appearance were sown in the greenhouse in individual rocket tubes in a standard greenhouse soil mix (UC Davis Metro Mix). Tubes were maintained in a moist environment. Germination was observed over the subsequent 2 years.

An additional set of 160 unburned and healthy fruits were collected from 10 parent trees. These fruits were subjected to one of seven heat duration treatments in the laboratory: 0, 5, 10, 20, 40, 60 and 90 s. Heat exposure was applied using a gas torch at an approximate distance of 5 cm. A thermocouple recorded this temperature to be 450 °C. This treatment was used to simulate the natural seasonal fires of the miombo ecosystems. Subsequently, each fruit was weighed, opened and seeds were extracted and then each seed weighed. Forty-four fruits were seedless (barren), 13 were damaged during extraction process, while 121 were healthy. These 121 seeds were planted in the greenhouse and their germination was observed for over 2 years. Two years was considered sufficient time to observe germination because seeds have been noted to remain in the soil for more than a year before they finally germinate (Van Daalen, 1991).

2.2. Non-husked seed preparation

Investigations of the effects fire on seed germination from within the protective fruit husk were also initiated. The goal of this experiment was to assess whether exposure to fire provided a positive impact on germination success from within fruits through scarification. We used 846 seeds collected from the Katavi ecosystem. These fruits that had been exposed to natural fire were scored for apparent burn intensity whereas unburned seeds we used in laboratory fire experiments.

Natural fire fruits ($n = 636$) were visually inspected, and placed into the following categories: (i) fruits from the previous year that had been burned by dry season fires from both that year and the previous year. These were easy to distinguish because they had been burned and covered by soil during the rainy season; (ii) fruits from that year that had fallen to the ground and been burned from early dry season fires; (iii) fruits that had recently fallen on the ground after the initial fires had swept through but were unburned. All three types of fruits were visually inspected and assigned burn classes from zero or one (depending on the experiment), being very lightly charred, to five or six (depending on the experiment), being completely blackened and fragile as a consequence of burning.

For the non-husked seeds, laboratory fire experiments involved 210 fruits that were collected unburned in the field. Fruits from each parent were subjected to seven heat duration treatments in the laboratory: 0, 5, 10, 20, 40, 60, 90 s of fire

exposure at 450 °C, as described above. Each fruit was weighed and sown in the greenhouse with their husks still intact to determine the effects of husking on seed germination.

At the conclusion of the experiment all 842 remaining unhusked seeds were harvested and examined. For the first 16 intact seeds encountered, we conducted a tetrazolium test for seed viability (Baskin and Baskin, 1998). All seeds responded positively to this test and were considered viable. Thenceforth, we simply scored seeds as still viable if the seed and seed coat remained intact upon opening the fruit. We then examined the likelihood of seed persistence based on different exposure to either field or laboratory fire treatments.

A multivariate logistic regression using burn duration, parent, fruit and seed mass to predict germination success was conducted using JMP 5.1 (SAS Institute, 1999).

3. Results

3.1. Husked seeds

The proportion of husked seeds that germinated, as predicted by our conceptual model, decreased with increased exposure to fire (Fig. 2). Among fruits experiencing fire under field conditions, germination rate was highest in least burned classes (1 and 2), despite many seeds collected from the field being categorized in more severe burn classes (3 and 4, Fig. 2). A logistic model regression of germination success by burn class failed to reach significance ($\chi^2 = 7.33$; d.f. = 4; $p = 0.12$). All germinated seeds, however, were from just 4 of the 10 parental trees sampled in the field. Adding parent identity to the logistic model resulted in a significant model ($\chi^2 = 27.72$; d.f. = 14; $p = 0.015$), however sample sizes of parents within burn classes were small and no individual parents emerge as significantly different from others.

We observed similar but less marked patterns of decreased survivorship and germination with increased heat exposure with controlled fire exposure (Fig. 3). A multivariate logistic model using burn duration, fruit weight, seed weight and parental identification to predict germination success yielded significant effects of burn duration and a marginal effect of fruit weight (Table 1). The insulating effect of fruits was apparent in that the

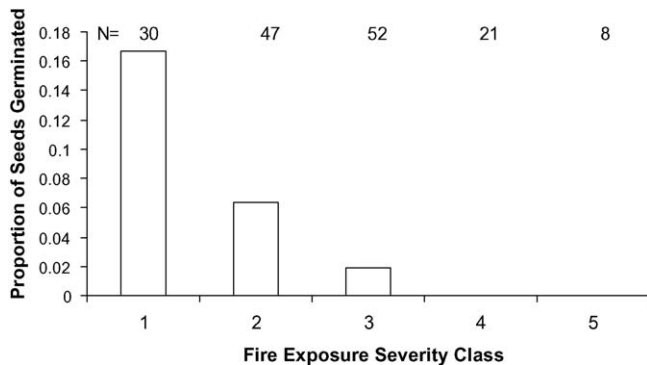


Fig. 2. The proportion of *P. angolensis* seeds germinated among fruit burn classes. Fruits were collected in the field and scored for fire exposure severity from 1 (slight charring) to 5 (severely blackened). All fruits were then husked and seeds were germinated in the greenhouse. Sample sizes are shown above.

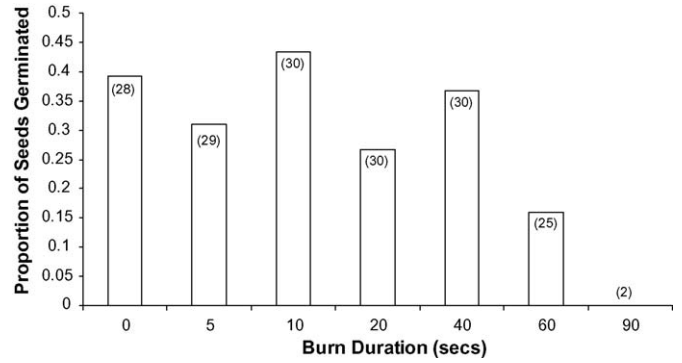


Fig. 3. Total proportion of *P. angolensis* seeds germinating after exposure of fruits to simulated fire. Simulated fire was done under laboratory conditions exposing fruits to 450 °C using a propane torch at a distance of approximately 5 cm. Time of exposure varied from 0 to 60 s for most seeds (~30 per treatment). Number of trials at each burn duration are reported in parentheses in bars. All fruits were then husked and seeds were germinated in the greenhouse.

fraction of seeds germinating within treatments remained mostly constant up through 40 s of exposure at 450 °C. In the planning of the experiment, we thought that 40 and 60 s of exposure to a direct flame heat would be adequate to cause increased seed mortality and so conducted very few ($n = 2$) trials at 90 s. Indeed, 90 s of exposure resulted in severe charring and seeds within these fruits were, in all but two trials, charred and obviously dead. Thus, we only planted and assessed germination in two cases. We expect that increasing this sample size would verify the result we achieved with the small sample presented here.

3.2. Non-husked seeds

The second set of experiments focused on understanding the degree to which exposure to fire may facilitate germination from within fruits. We planted 846 field burned seeds in their husks and allowed them to germinate for approximately 1.5 years, after which we harvested ungerminated fruits and opened them to assess remaining seed viability. An additional 210 unhusked seeds that were exposed to experimental fire treatments, 30 in each of 7 burn time periods, were planted. Our expectation, based on germination rates from husked seeds, was that unhusked seed germination rates would be very low.

Germination incidents were, indeed, rare. Nevertheless, a pattern emerged. No seeds germinated from within unburned

Table 1
Results of a multivariate logistical model predicting germination success of *Pterocarpus angolensis* seeds by experimental burn duration, fruit weight, seed weight, and parental tree

| | d.f. | χ^2 | p |
|-------------------------------------|------|----------|--------|
| Overall model | 14 | 27.72 | 0.0155 |
| Individual effects (Wald χ^2) | | | |
| Burn duration | 1 | 4.42 | 0.036 |
| Fruit weight | 1 | 3.13 | 0.077 |
| Seed weight | 1 | 0.87 | 0.352 |
| Parent ID | 9 | 11.47 | 0.345 |

Burn duration was achieved using a propane torch exposure of fruits to 450 °C for 0, 5, 10, 20, 40, 60 or 90 s.

Table 2

Fruit burn class and duration of successful seed germinations and remaining viable seeds among the non-husked seeds for both (a) natural fires and (b) laboratory experiments

| | Burn class | | | | | | |
|------------------------------|-------------------|----|-----|-----|-----|-----|----|
| | 0 | 1 | 2 | 3 | 4 | 5 | 6 |
| (a) Natural fire | | | | | | | |
| Number germinated | 0 | 0 | 3 | 2 | 0 | 0 | 0 |
| Number remaining viable | 0 | 0 | 10 | 3 | 0 | 0 | 0 |
| Total number planted | 183 | 36 | 198 | 148 | 100 | 102 | 48 |
| | Burn duration (s) | | | | | | |
| | 0 | 5 | 10 | 20 | 40 | 60 | 90 |
| (b) Experimental fire | | | | | | | |
| Number germinated | 0 | 2 | 1 | 1 | 1 | 0 | 1 |
| Number remaining viable | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| Total number planted | 30 | 30 | 30 | 30 | 30 | 30 | 30 |

husks, or remained viable for the duration of the experiment. In contrast, all 5 germinations and all 13 remaining viable seeds were from either burn class 2 or 3. No seeds from severely burned (class 4, 5 or 6) fruits germinated or remained viable for the duration of the experiment (Table 2a). Similarly, no unburned seeds germinated or remained viable for the duration of the experiment from the laboratory experimental seed trials. Germination, however, was more broadly distributed among the fruits exposed to laboratory fire, with germination and viability coming from seeds spanning treatment levels from 5 to 90 s (Table 2b). With small sample sizes, contingency table results for both experiments suggest a significant result, but are suspect because of low expected values and are, thus, not reported here.

4. Discussion

Our experiments focused on investigating the effects of fire intensity, husking, fruit and seed weight on the germination of *P. angolensis* seeds. We found general confirmation for our conceptual model (Fig. 1). First, among the husked seeds, germination success did, as predicted, decline with exposure to fire. Our results show that fruits appear to confer fire resilience to the seeds, with many seeds germinating despite exposure to 40 s of fire at 450 °C. This amount of fire exposure, for example, was sufficient to turn husks red hot.

In addition, we find evidence that fire is a requirement for germination as suggested by our model (Fig. 1). Not a single seed germinated from an unburned fruit out of a pool of over 200 trials. Naturally, our lab conditions vary from field conditions, so our germination rates may not reflect actual field germination rates, but the pattern remains that some exposure to fire assists in breaking down the woody fruit, facilitating germination.

P. angolensis grows in a fire climax ecosystem where current burning practices include an annual burn cycle. It is hardly surprising that this species carries adaptations to resist heat from surface fires. Our results suggest that the fruit capsule is, in fact, very resistant to brief heat exposure. In our experiment, exposure to moderate heat promoted higher germination rates.

Nonetheless, increasing germination failure with higher exposure to heat suggests some forms of fire management may exceed the capacity of this species to thrive. Sometimes burns occur in the middle or late in the dry season as a result of deliberate burning or lightning strikes resulting in a hot fire. High temperatures may be a major contributing factor to the lack of recruitment of the species in the wild (Caro et al., 2005). It is quite possible, though not established, that the current fire management regime is too frequent for good regeneration of this, and perhaps other, miombo species.

There is need for specific integrated field experiments to better understand the consequence of repeated exposure to fire on seed viability in miombo trees. Miombo ecosystems often experience variable precipitation patterns (Chipika and Kowero, 2000). Wet periods may foster increased plant biomass and subsequent more severe fires, but these periods may also be favorable periods for seedling germination and establishment. In contrast, droughts may result in reduced plant biomass, reduced fire severity, but increased water stress on those seeds that germinate.

Poor germination was observed among seeds that were planted in the husk regardless of whether they were collected already burnt in the field or exposed to fire in the laboratory. *Pterocarpus* fruits are very hard and membranous. They require scarification and degradation in order for seeds to germinate. This is confirmed by other studies conducted on other savanna woodland species (e.g. Walters et al., 2004) that have observed that hard fruits require a physical mechanism to crack them open in order to allow water in and soak the seed, thereby triggering the germination process. Mbalo and Witkowski (1997) also observed that heat shocks provoked by the passage of fires could be one of the principal natural agents enabling the breaking of seed dormancy and subsequent germination. Sensitivity to fire combined with poor germination of seeds remaining in their husks suggests that germination is difficult in the wild. Thus, natural fire is almost certainly an important contributor to successful germination in *P. angolensis*.

Human application of fire is not recent in Africa. How anthropogenic fire has altered selection pressures for miombo species is unclear. A shift in fire management may have important implications for forest regeneration. Early dry season fires set by management authorities are likely to cause lower direct mortality to seeds in woody fruits because they tend to be cooler. Yet these early, cooler fires may have a differential affect on seedling survivorship as well, and it may be in the opposite direction if fires occur before seedlings and saplings have gone dormant for the dry season. Fire management for forest health in this region requires additional careful study of several life stages of several tree species before one could make a definitive recommendation regarding fire.

It is unclear why *P. angolensis* seeds that were removed from husks took a long time to germinate but there may be other factors that influence the breakage of dormancy beyond physical rupturing of the fruit such as that facilitated by fire. Large seeds when wet and in the soil might be susceptible to predation and fungi although this does not seem to be the case with *Pterocarpus* (Van der Reit et al., 1998). High levels of dormancy of seeds that sit in the soil for a long time before they

germinate have been observed in other leguminous species of savanna woodlands (Bebwi and Mohamed, 1985; Chipika and Kowero, 2000). Such dormancy has recently been attributed to the rainfall cycle (Chipika and Kowero, 2000) and longevity of the species of 150 years (Boaler, 1966; Stahle et al., 1999), such that the recruitment of new cohorts may be spread across many years. Further investigations need to be carried out in order to understand the recruitment ecology and sustainable management of this commercially important tree species in miombo ecosystems.

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