Effects of fire, bruchid beetles and soil type on germination and seedling establishment of Acacia drepanolobium

B.D. Okello^{1,3} and T.P. Young²

¹University of Natal, Department of Range & Forage Resources, Private Bag X01, Scottsville, 3209 Republic of South Africa

²Correspondence address: University of California, Davis, Department of Environmental Horticulture,

Davis CA 95616, United States of America; E-mail: tpyoung@ucdavis.edu

Received 02 November 1998; Accepted 16 November 1999

Abstract

The effects of fire, bruchid seed beetles and soil type on the germination and seedling establishment of Acacia drepanolobium were experimentally investigated. Seeds subjected to three seed treatments (bruchid damaged, bruchid-free burnt, and bruchid-free unburned) were germinated in three different soil types (black cotton. red sandy, and clay loam soils). Undamaged seeds had significantly higher germination (85.3%), than either beetle damaged (20.6%), or burnt seeds (3.4%). Soil type did not influence germination or seedling survival. Burnt seeds had an average germination of 2% in clay loams and 5.4% in red sandy soils, while beetle damaged seeds had an average germination of 15.6% in clay loams and 28.7% in black cotton soils. Treatment effects on seedling mortality or survival were not significant but seedlings from undamaged seeds had higher survival rates than those damaged by bruchid

³Current address: Mpala Research Center, P.O. Box 555, Nanyuki, Kenya; E-mail: gmc@africaonline.co.ke

Additional index words: Arid uplands, black cotton soils, Kenya, Laikipia, regeneration

Introduction

Acacia drepanolobium forms nearly mono-dominant stands in many arid uplands with impeded drainage in East Africa. Belsky (1990) suggested that other species of trees and shrubs do not occur on the poor drainage and anaerobic conditions of these high clay soils. Moreover, it is possible that A. drepanolobium can only establish on these soils. In the Laikipia plateau of north-central Kenya, A. drepanolobium forms a virtual monoculture, often comprising more than 90% of the total tree and shrub density in the black cotton soils (Young et al. 1997; Young et al. 1998). drepanolobium can be either a tree or shrub, that grows to 7.5m in height, and has swollen thorns that are inhabited by ants (Crematogaster mimosae, C. nigriceps, C. sjoestedtii and Tetraponera penzigi) (Coe 1993; Young et al. 1997). Both ants and bruchid beetles feed on the seeds of A. drepanolobium (personal observations).

Increase in woody cover of Acacia woodlands often leads to a decline in the productivity of understorey grass or herb layer species (Sabiiti & Wein 1988; Sabiiti & Edroma 1991), though not exclusively so (Cavanagh 1980; Belsky 1990). Bush encroachment also limits the area grazed by inhibiting free movement of grazers to feed within bush thickets. Pastoralists frequently burned Acacia-dominated woodlands as a bush control measure and also to enhance fresh growth of forage (Pratt & Gwyne 1977; Pellew 1983). Fires are currently infrequent at the study site. Acacia drepanolobium coppices readily when harvested (Okello et al. 2001) or burned (Okello et al. in review).

Many Acacia trees and shrubs regenerate both vegetatively (Purdie & Slaytor 1976; Jacoby 1986; Hodgkinson & Oxley 1990) and from seed (Oba 1990), the latter being the dominant mode (Mucunguzi 1995). Germination and seedling establishment can be influenced by fire (Hodgkinson & Oxley 1990; Portlock et al. 1990), temperature (Hodgkinson 1986), soil moisture (Hodgkinson & Oxley 1990), seed coat thickness (Fenner 1986), predation (Sabiiti & Edroma 1991), competition (Cavanagh 1980), intrinsic ability of a species to germinate and establish (Fenner 1986), and seed size (Mucunguzi 1995) and shape (Cavanagh 1980). Most indehiscent Acacia species need seed pre-sowing treatment before germination (Lamprey 1967), but many dehiscent species germinate freely without pre-sowing treatment, especially if they are fresh (Cavanagh 1980). Some species germinate after a fire (Hodgkinson & Harrington 1985). This may be reflective of the means by which the two types are dispersed. Most dehiscent species are dispersed by wind, while indehiscent ones are mostly dispersed by herbivores.

Fire is a frequent occurrence in East African savannas (Wein & Edroma 1986) and it is one of the most potent environmental factors shaping the structure of its vegetation (Oba 1990). Fire events may stimulate (Hodgkinson & Harrington 1985) or enhance (Pratt & Knight 1971, Hodgkinson & Oxley 1990) germination of some tree and shrub species. Fire may also inhibit germination and stifle seedling establishment of some Acacia species by killing them (Cavanagh 1980). Fire has therefore been used as a tool in range management by pastoralists, ranchers, and scientists (Hodgkinson 1986; O'Connor 1985). The effect of fire on the

germination and seedling establishment of any species will depend on the species physiological and morphological adaptations to fire (Oba 1990; Hodgkinson 1986; Hodgkinson & Oxley 1990), the amount and type of fuel used, and the frequency and intensity of fires (Noble et al. 1986; Belsky 1990).

Seeds of almost all Acacia species are consumed or attacked by bruchid beetles (Miller 1995; Miller & Coe 1993) and an Acacia species may be utilized by one or a number of Bruchid species (Coe & Coe 1987). The number of bruchid species utilizing any Acacia species tends to be proportional to the seed size (Halevy 1974). The extent of destruction of the seed and food reserves by bruchid beetles and, by implication seed size, are important in seed viability after bruchid infestation (Lamprey et al. 1974). Seeds germinated after the first instar larvae are likely to have a higher germination rate than those in which adult bruchid beetles emerge. The bruchid beetle that infests A. drepanolobium was identified at the National Museums of Kenya to the genus level as a Bruchus sp. (John Njoroge, personal communication). Only one species was found, and each seed of A. drepanolobium was attacked by only one individual of Bruchus sp. The adult Bruchus sp. leaves a large deep hole (almost three quarters of the seed surface on one side) upon emergence. The adult emerges after consuming most of the seed contents.

The purpose of this study was to determine the effect of (1) seed damage by bruchid beetles, (2) fire, and (3) soil type on the germination and seedling establishment of A. drepanolobium. We first conducted a pilot study to determine the germination potential of A. drepanolobium seeds by examining the effect of acid-scarification on germination of bruchid-damaged and undamaged (control) seeds, and on undamaged (by bruchids) burnt seeds. We then tested the hypotheses that fire and bruchid infestation enhances germination of A. drepanolobium, and that seedling establishment and survival of A. drepanolobium differs with soil type. The latter hypothesis would test whether A. drepanolobium is specialized only for black cotton soils.

Procedure

The study was conducted in a screen house at Mpala Research Center in north-central Kenya. The Center is located at 26°54'28"E, 0°18'30"N. Altitude ranges from 600 m to 1 800 m above sea level. Year to year variation in rainfall is high and annual rainfall averages 500-550 mm. Maximum temperatures range from 25°C to 33°C and minimum temperatures from 12°C to 17°C. The Center has two predominant soil types; heavy clay black cotton' soils, which cover most of the Laikipia streau (Taiti 1992), and red sandy soils (Ahn & Geiger 1987). Intermediate clay loamy soils occur along the coundary of black cotton and red sandy soils. Acacia Panolobium dominates the overstorey vegetation in the black cotton soils, while Acacia etbaica, Acacia Previspica, Acacia mellifera, Acacia nilotica and Aca-

cia gerardii are found in the sandy soils. All these species are present in the intermediate clay loams.

Seeds of A. drepanolobium were harvested from trees with mature pods at Mpala between May and July 1996. The seeds were sorted into bruchid damaged and undamaged seeds by observing for the presence or absence of bruchid entry and exit holes, and ant damage to the seed testa. The seeds were stored in polythene bags and the undamaged ones examined again for signs of damage after two weeks.

Effect of scarification by 1M hydrochloric acid on the germination of Acacia drepanolobium

The pilot experiment was carried out to determine how burnt, beetle-damaged and undamaged seeds of A. drepanolobium respond to an acid pre-sowing scarification treatment. For the burnt seeds, a light grass fire (150 g of dry grass) was passed through a batch of 200 undamaged seeds placed on the ground. One hundred and twenty of these seeds were randomly picked and divided into two lots of 60 seeds each. One hundred and twenty bruchid-damaged seeds were picked and similarly divided into two batches, and 120 beetle-free, unburned (control) seeds were also divided into two equal lots. One set of 60 seeds from each of the three treatments was separately immersed into jars containing 1M HCl for five minutes and were then rinsed with rainwater. The two sets, acid-scarified and unscarified, were then germinated on filter paper lined trays. Each filter paper had twenty seeds. Scarified and unscarified seeds were germinated on separate trays. The trays were moistened with water on a daily basis and covered with a polythene bag to keep the trays moist. The germination trial was conducted inside a screen house where the temperatures ranged from a minimum of 17°C to a maximum of 33°C. Germination was recorded daily for thirteen days. Germination was deemed to have occurred when the radicle extended to 2 mm. After 13 days all the seeds that had not germinated were found to have rotted and were discarded.

This was a nested experiment (Steel & Torrie 1981), with the acid being the major treatment, while burnt and damaged seeds as the minor treatments. Analysis was conducted using Systat® software.

Effects of fire, bruchid seed beetles, and soil type on germination and seedling establishment

Three soil types (black cotton, red sandy, and an intermediate clay loamy soils) were collected to a depth of 20 cm and placed in wooden germination crates. The crates were 0.5 m x 0.5 m x 0.15 m deep, and were subdivided into 49 equal squares using nylon threads. These crates were watered daily for two months to test for the soil seed bank. Emerging seedlings were mainly herbs and A. brevispica from the red sandy and clay loams. All seedlings were removed. None of the seedlings was A. drepanolobium. Twenty-seven crates were used in nine treatment combinations each replicated three times. The treatments were (1) burnt seeds,

Table 1 Mean percent germination and Standard Error of three treatments of *Acacia drepanolobium* seeds with and without 1-M hydrochloric acid treatment. n=60 seeds in each treatment combination, split into three replicates

Acid-treated	Control	
10.0 ± 0.0	10.0 ± 2.9	
3.3 ± 1.6	0.0 ± 0.0	
73.0 ± 9.2	78.0 ± 4.4	
	10.0 ± 0.0 3.3 ± 1.6	

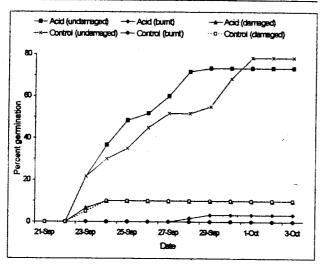


Figure 1 Percent germination of burned, bruchid-damaged and undamaged seeds of *Acacia drepanolobium* with and without 1 M hydrochloric acid pre-germination treatment.

(2) bruchid damaged seeds and (3) undamaged (control) seeds in each of the three soil types in a modified factorial design (we did not include burnt damaged seeds as a treatment). One seed was planted at a depth of 1 cm in each of the 49 squares in all the crates. One hundred and forty-seven seeds were used in each treatment combination (1 323 seeds in total). For seven days germination was recorded daily by observing for emergence of the plumule. After the first seven days, germination and seedling growth (measured by increase in heights to the nearest 0.1 cm) were recorded on a weekly basis. Since there were no significant interaction effects, the different effects were analyzed separately and means differentiated by Tukeys post hoc test using Systat® software.

Results

Influence of hydrochloric acid on seed germination

Acid treatment had no significant influence on the total germination of Acacia drepanolobium seeds (P=0.88; Table 1, Figure 1). However, acid-treated normal seeds germinated more quickly than the controls (Figure 1). On average, control seeds took 35% longer to germinate (5.4 days) than scarified seeds (4.0 days). Burning and bruchid damage significantly reduced germination of A. drepanolobium seeds (P<0.001) compared to undamaged ones.

Table 2 Mean percent germination and Standard Error of three treatments of *Acacie drepenolobium* seeds under different soil types. n = 147 in each treatment combination in three replicates of 49. Total number of seeds 1323

Soil / seed type	Damaged	Burnt	Undamaged
Red	17.7 ± 4.1	5.4 ± 1.8	89.2 ± 2.4
Loam	15.6 ± 4.1	2.0 ± 1.2	77.5 ± 10.8
Black Cotton	28.7 ± 16.7	2.7 ± 1.4	86.4 ± 2.7
Mean	20.7 ± 4.1	3.4 ± 1.0	84.4 ± 3.5

Table 3 Mean percent survival and Standard Error (5%) of seedlings from three *Acacia drepanolobium* seed treatments under different soil types. n = 147 seeds in each treatment combination, in three replicates of 49. Total number of seeds 1323

Soil / seed type	Damaged	Burnt	Undamaged
Red	94.6 ± 2.9	99.3 ± 0.7	89.1 ± 3.8
Loam	91.8 ± 4.2	98.0 ± 1.2	86.4 ± 6.5
Black Cotton	77.5 ± 1.5	100.0 ± 0.0	91.8 ± 1.2
Mean	87.9 ± 5.3	99.1 ± 0.6	89.1 ± 1.6

Effects of seed and soil type on germination and seedling establishment

Germination and growth of seedlings were monitored for 19 weeks. There was no significant interaction between the seed treatments and soil type on seed germination and seedling establishment (P=0.68). Percent germination was significantly different among the three seed treatments (P < 0.001). Germination was highest for undamaged seeds and lowest for burnt seeds (Table 2). These results are consistent with those from the pilot experiment reported earlier, bruchid damaged seeds had a significantly higher percent germination compared to burnt seeds (P=0.02). Soil type did not influence seed germination (P=0.39). Bruchid damaged seeds took a mean of 8 days to germinate compared with 8.9 and 11.3 days for undamaged and burnt seeds respectively. The only significant difference in time to germination was between bruchid damaged and burnt seeds (P=0.048).

Growth rates of the three seed treatments were similar, and no interaction of factors was found. By the 16th week average growth measured in terms of height, was marginally higher in the mixed soil (13.6 cm) compared to the black soil (13.1cm). Undamaged (control) seeds also showed marginally higher growth (in all soil types) up to the 16th week. Growth rates of seedlings from undamaged seeds were high at the beginning but began to decline after 12 weeks. The slack in the growth rates of seedlings from this treatment was probably due to overcrowding and intense competition for nutrients. There was an average of 40 seedlings in an area of 0.025 m² (density of 1 600 m⁻²) for seedlings from undamaged seeds. During the course of growth nutrients may be depleted, and this probably leads to slower growth rates. Seedlings from burnt seeds had consistently slower growth. However, this increased

with time. At the 19th week, the growth rate of these seedlings was still increasing. This is probably due to the low seedling density and therefore less competition for nutrients. At the end of the 19th week, seedlings from the damaged seeds had an average height of 17.5 cm compared to 17.2 cm and 14.4 cm for burnt and undamaged seedlings respectively.

Seedling survival showed no significant differences between seed treatments (P<0.65) or between soil types (P=0.07; Table 3). Among seedlings that died, those from undamaged seeds on average survived longer (23 days), than those from burnt (18 days) and bruchid damaged seeds (11 days).

Discussion

The ability of a species to replace itself is of major ecological and economic importance (Cavanagh 1980). Germination and early growth are the major phases in the population dynamics of *Acacia* species (Halevy 1974; Fenner 1986). These processes determine the density and distribution of *Acacia* species (Oba 1990), owing to the high mortality that characterise them (Coe & Coe 1987).

Acacia drepanolobium seeds do not need scarification or pre-sowing seed treatment to germinate. This is consistent with the widely held view that seeds of dehiscent Acacias germinate readily without need for scarification (Lamprey et al. 1974). In the pilot study, both scarified and non-scarified seeds had similar rates of germination. However, the scarified seeds took a shorter time to reach peak germination compared to the control.

Bruchid damaged seeds took a marginally shorter time to germinate compared to undamaged and burnt seeds. The time differences recorded in both the pilot and main experiment were however small, and may not be important in field germination. This result suggests that acid treated and bruchid damaged seeds may take advantage of conducive germination conditions marginally faster than the other seed types. This may be important in areas where conditions conducive to germination are short lived.

Fire killed most of the A. drepanolobium seeds. Both germination trials recorded marginal rates of germination for burnt seeds. Hodgkinson & Oxley (1990) argued that fire promotes germination for some species by the action of its heat, which opens the lens behind the helium, an act that allows in water and results in germination. The heat is believed to soften and break open the seed coat (Sabiiti & Wein 1988). Coe & Coe (1987) postulated that fire events in the savanna were likely to be a means of increasing water permeability of the testa. However, high fire temperatures kill seeds. Hodgkinson & Oxley (1990) reported that seeds of icacia aneura were killed at fire temperatures exceeding 80°C. There seems to be a threshold temperature beyond which fire kills seeds, but this varies from

species to species (Ramsey & Oxley 1996). Cavanagh (1980) reported that Acacia seeds could withstand prolonged periods of exposure to dry, but not to moist heat. They found most seeds dead at temperatures of 110-120°C when exposed for short periods. Despite its reported effects on seed germination, fire is not a pre-requisite for field germination (Cavanagh 1980). In the present study, fire temperature was not recorded but the fuel load was low. There is a possibility that the fire temperatures attained exceeded the threshold limit for A. drepanolobium seeds that have a thin seed coat, A. drepanolobium being dehiscent (Lamprey et al. 1974). In the field, fire temperatures easily reach 300°C and temperatures of 500°C have been recorded (Ramsey & Oxley 1996). However, given that germination from control seeds were quite high, it is unlikely that fire plays a significant role in enhancing germination of A. drepanolobium seeds. Rather, this result suggests that fire can be an important tool in the control of A. drepanolobium regeneration from seed. Fire may kill the seeds thus preventing germination, this will then significantly suppress recruitment of new seedlings. This has important consequences in the population dynamics of acacias which mostly regenerate from seed to effectively propagate (Harper 1982). Burnt seeds also took slightly longer to germinate than the other two treatments, while damaged seeds took a shorter time to germinate.

Bruchid beetles that feed on A. drepanolobium seeds significantly limit their germination potential. Seeds that germinate may not have enough reserves to survive competition and establish. Percent germination of damaged seeds in this study was much lower than the control. The higher mortality recorded in the seedlings from bruchid damaged seeds suggest that the seedlings may be weak as a result of depleted food reserves during early growth due to infestation by the Bruchus sp. which consume a substantial portion of the seed food reserves.

Bruchid larvae are predators of the seed reserves and can therefore influence the germination rate of Acacia seeds (Halevy 1974; Lamprey et al. 1974; Miller 1995; Miller 1994c). Some authors (Lamprey et al. 1974; Halevy 1974) have suggested that the holes created by the bruchid larvae enhance permeability of the seed testa and hence have a positive effect on Acacia seed germination. Others, Miller (1995, 1994b); and Mucunguzi (1995) have reported no difference in germination rates between bruchid damaged and undamaged seeds of Acacia nilotica, Acacia tortilis and Acacia hebeclada. All these species are indehiscent. Lamprey et al. (1974), Mucunguzi (1995), and Halevy (1974) reported 6% germination in bruchid damaged seeds of Acacia gerardii, a dehiscent species. Germination of bruchid damaged seeds in this study was 10-20% higher. Mucunguzi (1995) concluded that bruchid beetles promoted early germination and establishment of Acacia sieberana. He recorded a 17% germination in bruchid damaged seeds, and no germination in undamaged

seeds, yet when the undamaged seeds were pre-treated with 1M HCl germination reached 80%. workers such as Halevy (1974) and Lamprey et al. (1974) thought that the exit holes of adult bruchid beetles were used for water imbibition. But recent evidence by Miller (1994a, 1994b, 1994c) suggests that seeds with exit holes are in most cases unviable since most of the food reserves have been consumed, and water primarily enters the seeds via the larval entry holes. In general, bruchid damage adversely influences germinability of most Acacia seeds (Mucunguzi 1995), though not exclusively so. The cost of bruchid damage, which results in reduced seed viability potential, may be compensated for by the production of large numbers of seeds (Halevy 1974; Lamprey et al. 1974). Survival was much lower, though not significantly so, in seedlings from damaged seeds compared to those from undamaged and burnt seeds.

Acacia species (e.g. A. gerardii) are believed to have evolved mechanisms that enhance the germination of their seeds by producing large amounts of pods and seeds (Halevy 1974; Lamprey et al. 1974). Halevy (1974) reported that A. tortilis showed a temporal scatter in germination, and argued that this phenomenon increased its chances of survival under variable and erratic conditions of their environment. In this study, seeds of A. drepanolobium also showed a temporal scatter in germination, with a range of 2 to 15 days.

Acacia drepanolobium may be expected to be adapted to fire. It occurs in ecosystems prone to fire, it coppices readily after being burned or cut, and older stems have relatively thick bark. Nonetheless, seeds of A. drepanolobium do not appear to be either fire dependent or even fire tolerant. Of course, fire temperatures drop rapidly at ground level, so even shallow burial may protect these seeds from lethal fire temperatures.

Throughout East Africa, A. drepanolobium is largely restricted to black cotton and similar heavy clays of impeded drainage, where it forms a virtual monoculture. In central Laikipia, this soil restriction is abrupt and Two alternative hypotheses are possible. First, A. drepanolobium may be unable to germinate, establish and grow on different soil types. Second, A. drepanolobium may be uniquely adapted to these specialized soils, and although it can grow on alternative soils in green house conditions, it may be at a disadvantage in such soils due to competition by other tree and shrub species which are better adapted to the soils. Our results show that the alternative major soil type in Laikipia does not restrict the germination or establishment of A. drepanolobium. While it remains possible that such a restriction occurs at a later life stage, this is unlikely. For example, A. drepanolobium trees are not found beyond the narrow ecotone of community and soil types in Laikipia. It is more likely that the restriction to black cotton soils is related to the competitive conditions in alternative communities. In fact, elsewhere in East

Africa (and even Laikipia), A. drepanolobium can sometimes be found in alternative soil types (personal observation).

We have shown that A. drepanolobium can readily germinate and establish in different soil types and not necessarily in black cotton soils only. It is not known why it is virtually absent from red sandy soils of Laikipia. One possibility is that it is a poor competitor when growing on soils other than black cotton soils. We have also shown that both fire and Bruchus sp. significantly limit regeneration of A. drepanolobium from seed. Seed damage by Bruchus species also enhances mortality of seedlings during early periods of establishment.

Acknowledgments

We are very grateful to Citibank Mpala Fellowships, the International Foundation for Science, the National Geographic Society, the Smithsonian Institution, and L. Scott for the research grants that enabled us undertake this project. We thank G. Small, J.W. Smith, and N. Georgiadis, Director, Mpala Research Center, for all the assistance accorded us during the study. We acknowledge the assistance provided by M. Mungai of the National Museums of Kenya, and through him, J. Njoroge who helped us in the identification of the bruchid beetle. Comments from T.G. O'Connor greatly improved this manuscript. We acknowledge the contribution of many ranchers who shared with us their knowledge of Acacia drepanolobium. Finally, our gratitude goes to D. Kinyua and our field assistants, F. Erii and S. Ekwang'a.

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