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Impact of bush fire on germination of some West African acacias

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Abstract

Bush fire is a widespread and recurrent feature of the African dry savannas and contributes largely to changes in the composition of vegetation communities. However, the impact on seed regeneration in local species has received little attention. This study evaluates the effects of managed bush fire on seed viability and germination capacity for 10 species of West African acacia (sensu lato), taking into consideration fire intensity (related to the quantity of combustible biomass) and seed location (in, on or above the soil) at the time of the fire.

The results indicate that the behavior of different species is related to their taxonomic position. *Acacia* species belonging to the sub-genus *Aculeiferum* are characterized by their lack of integument inhibition. The consequences of the passage of fire, depending on the intensity of heat shock, are limited to seed survival: they either retain viability or die. Seeds from the sub-genera *Acacia* and *Faidherbia albida* have a hard integument that needs to be scarified in order for germination to ensue. In our study, we show that on the whole, heat shocks cannot scarify the integument of the seeds without resultant lethal damage to their embryos. This is true regardless of seed status (naked or protected by seed pods), seed location (in, on or under the soil) and fire intensity. The only species to manifest an improvement in germination capacity, under certain selective experimental fire conditions, and in relation to the non-scarified control are *A. raddiana*, *A. seyal* and *A. sieberiana*. Nevertheless, germination remains substantially inferior to that obtained after scarification by removal of a small piece of integument.

It thus seems conceivable to conclude that, contrary to what takes place in Mediterranean climate ecosystems and the wet tropics, fire does not encourage the in situ germination of different *Acacia* species. This finding implies that in dry savanna areas, it is not possible to regard fire as an accessory to reforestation or natural regeneration of these species.

Keywords: Bush fire; *Acacia* spp.; *Faidherbia* spp.; Germination; Seed dormancy; Savanna; West Africa

1. Introduction

Bush fires, whether of natural or anthropic origin, are an essential feature in regeneration and modification of vegetation communities (Gillon, 1983; Geerling, 1985; Monnier, 1990; Kozlowski, 2000). In tropical

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savannas, the principal effect of fire on the floristic composition has been the elimination of sensitive species, which have been driven back into wetter habitats (gallery forest) and areas of discontinuous growth (hill and rock), and a predominance of resistant species. These species have developed various adaptive strategies, amongst them, the hide-and-resprout strategy which allows them to regenerate from subterranean vegetative organs and the stay-and-resist strategy in which they develop protective structures against fire (trunk and bark thickening) (Monnier, 1968; Gignoux et al., 1997).

In Sahelian and Sudanian savannas, there are numerous acacia, leguminous trees, shrubs or creepers belonging to the *Acacia* and *Faidherbia* genera. These species colonize savannas by producing vast quantities of seed: for certain species, it has been possible to count as many as several hundred seeds per square meter (Sabiiti and Wein, 1987; Tybirk et al., 1994). They frequently have hard, impermeable seminal integuments, which ensure dormancy and are well adapted to long-term survival and dispersal strategies (Coe and Coe, 1987; Sabiiti and Wein, 1987; Gutterman, 1994; Danthu et al., 1996; Vassal, 1998). Heat shocks provoked by the passage of fires could well be one of the principal natural agents enabling the breaking of seed dormancy and subsequent germination, as has already been demonstrated for various Mediterranean legumes (Portlock et al., 1990; Tarrega et al., 1992; Bradstock and Auld, 1995), in some wet tropical regions (Saharjo and Watanabe, 1997), and arid and semi-arid zones (Pieterse and Caims, 1986; Sabiiti and Wein, 1987; Oba, 1990; Cox et al., 1993). However, such windows of fire intensity (temperature, duration) as to allow breaking of dormancy for a given species, often prove to be limited (Portlock et al., 1990; Bradstock and Auld, 1995). Some studies have even indicated that the passage of fire has minimal influence on the regeneration of ligneous species such as *Dichrostachys cinerea*, *Acacia constricta* and *Prosopis velutina*, for which heat shock would not be able to scarify the seed integument without lethal embryo damage (Brown and Booysen, 1969; van Staden et al., 1994).

There has been very little work devoted to the impact of fire on the fate of seeds in Sudanian and Sahelian zones. Yet, these ecosystems are very frequently overrun by fire (Monnier, 1990). It is for this reason that we have concentrated our investigation on evaluating the consequences of bush fire on seed regeneration in different species of West African acacia. The main elements to be tested in this study involved *Acacia* species, their taxonomic position, their mode of dissemination and the presence of protective seedpods. Two main variables were tested: heat intensity and seed position. Fire intensity is dependent on the quantity of available combustible material. It is estimated that gramineous biomass must reach around 1 t of dry matter per hectare in order for fire to propagate. In savannas, the quantity of dry grassy biomass has been estimated at between 0.6 and 2–3 t ha^{-1} in the Sahelian region and can go up to 12 t ha^{-1} in the forest savannas (Gillet, 1967; Monnier, 1990). During bush fire, the rise in air temperature is transient (limited to the moment of passage of the fireline). Maximum temperatures are attained (sometimes exceeding 500 °C) some 10 cm above the ground, falling rapidly with height (Pitot and Masson, 1951; Monnier, 1990). The rise in soil temperature, which is limited to the superficial strata, is always low, but can last several quarters of an hour. As for the position of seed, three situations were considered: (1) more or less deeply buried in the soil, (2) on the surface or (3) suspended in the grass cover after dissemination or within the canopy (Sabiiti and Wein, 1987; Trabaud and Oustric, 1989; Oba, 1990). In fact, for a number of species with relatively late dehiscent pods, the seeds, suspended by a robust folded funicle, are also able to endure in the canopy even after the pod has opened (Coe and Coe, 1987).

2. Materials and methods

The 10 *Acacia* species (sensu lato) compared in this study were collected from natural stands in Senegal and Mauritania, with the exception of *A. kamerunensis*, which was obtained from an arboretum in Dakar. We used the taxonomy and nomenclature from Vassal (1998).

There were nine species belonging to the genus *Acacia* (sub-genus *Aculeiferum* and *Acacia*, the only representatives of the *Acacia* genus in the native African flora) (Table 1). They are as follows: *A. ataxacantha* DC; *A. dudgeoni* Craib ex Holl.; *A. ehrenbergiana* Hayne; *A. kamerunensis* Gandoger (synonym *A. pennata* (L.) Willd.); *A. nilotica* (L.)

Table 1
Some characteristics of the species used in the study (Brown and Booysen, 1969; Coe and Coe, 1987; Danthu et al., 1992; Tybirk et al., 1994; Vassal, 1998)

Species	Ecologic and bioclimatic zone	Origin of the seed lots	Tree habit	Pod dehiscence	Seed dispersal agencies
Genus *Acacia*, sub-genus *Aculeiferum*					
A. ataxacantha	Sahelo-Sudanian to Sudano-Sahelian	Bandia (14°36′N, 17°02′W)	Creeper	Dehiscent	Wind
A. dudgeoni	Sudano-Guinean	Bandafassi (12°32′N, 12°22′W)	Shrub	Dehiscent	Wind
A. kamerunensis	Guinean	Dakar (14°40′N, 17°28′W)	Creeper	Dehiscent	Wind
A. senegal	Sahelian to Sudano-Sahelian	Vélingara (15°00′N, 14°41′W)	Shrub	Dehiscent	Wind
Genus *Acacia*, sub-genus *Acacia*					
A. erhenbergiana	Sahelo-Saharian	Rkiz (16°57′N, 15°25′W)	Shrub	Dehiscent	Wind
A. nilotica	Sahelo-Saharian to Sudano-Guinean	Dahra (15°22′N, 15°30′W)	Tree	Indehiscent	Animal
A. raddiana	Saharian to Sahelian	Rao (15°54′N, 16°23′W)	Tree	Dehiscent	Wind/animal
A. seyal	Sahelo-Saharian to Sudano-Sahelian	Vélor (14°04′N, 16°16′W)	Tree	Dehiscent	Wind/animal
A. sieberiana	Sahelian to Sudanian	Sokone (13°55′N, 16°18′W)	Tree	Indehiscent	Animal
Genus *Faidherbia*					
F. albida	Sahelian to Guinean	Dangalma (14°44′N, 16°34′W)	Tree	Indehiscent	Animal

Willd. ex Del. subsp. *adstringens* (Schumach. and Thonn.) (synonym *A. nilotica* var. *adansonii* (Guill. and Perr.) O. Kuntze.); *A. raddiana* Savi, (synonym *A. tortilis* (Forssk.) Hayne subsp. *raddiana* (Savi) Brenan var. *raddiana*); *A. senegal* (L.) Willd.; *A. seyal* Del.; *A. sieberiana* DC. The 10th species is *Faidherbia albida* (Del.) A. Chev. (synonym *A. albida* Del.), belonging to the monospecific genus *Faidherbia*.

Table 1 defines some of the ecological characteristics of the different species and in particular the mode of dissemination of their seeds.

The experiments were carried out at the Dakar-Hann station in May and June 2000, during the dry season, with light or no wind and an ambient temperature of 25–30 °C, on dry, sandy soil.

The main parameters tested were as follows:

- *Seed position*: The position could be buried in the soil, on the soil or above the soil. The range tested (taking soil level as reference 0 and negative values buried) was as follows: −5, −2, 0, 10, 50, 100, 150, 300 and 450 cm.
- *Fire intensity*: In this paper, intensity is related only to fuel load per area unit (composed essentially of straw from *Schoenefeldia gracilis* Kunth.): $100\ \mathrm{g\ m^{-2}}$ (light), $300\ \mathrm{g\ m^{-2}}$ (medium) and $500\ \mathrm{g\ m^{-2}}$ (heavy) corresponding to 1, 3 and $5\ \mathrm{t\ ha^{-1}}$. The area ignited covered $31\ \mathrm{m^2}$ (a square with sides of 5.6 m). Maximum temperatures achieved at each level were recorded by thermal ribbons (Thermax® Six Levels Mini Stripes, measurement range 29–260 °C) (Table 2). Fire line speeds varied between 50 and $200\ \mathrm{m\ h^{-1}}$, according to fire intensity.

Four experiments were carried out.

In the first one, the objective was to evaluate seed hardiness of each species by comparing germination capacity of intact seeds and seeds for which seed coat

Table 2
Maximum temperatures (°C) measured during simulated fires in Senegal

Seed position (cm)	Fire intensity[a]		
	Low	Medium	High
Buried in the soil			
−5	<29	<44	<44
−2	<44	46–54	54–65
Placed on the soil			
0	>260	>260	>260
Placed above the soil			
10	216–224	>260	>260
50	193–199	>260	>260
100	154–160	232–241	>232
150	65–88	160–199	182–188
300	49–54	88–93	93–99
450	49–54	60–65	60–65

[a] Fire intensity has been related to fuel loads only.

inhibition has been eliminated by removal of a small piece of integument (2–4 mm^2) with pruning shears (Danthu et al., 1992; Diallo et al., 1996).

In the second experiment, seed viability after the passage of fire was assessed using a protocol in which seeds, after fire treatment, were scarified in order to eliminate seed dormancy and then sown. Germination capacity of seed lots under these conditions gives an indication of seed viability.

The third experiment tested the effect of fire on the breaking of seed dormancy. It concentrated exclusively on the treatments which had preserved seed viability in the second experiment. After the passage of fire, seeds were sown directly and germination compared to that of intact seeds.

The fourth experiment concerned more specifically the three species with indehiscent seed pods (*A. nilotica*, *A. sieberiana* and *F. albida*). It consisted of subjecting seed pods to high intensity fire then extracting the seeds. Their survival and germination capacity was then assessed.

Germination tests were carried out in germination boxes, on a bed of sterilized sand, in the dark, at 30 °C (Danthu et al., 1992). A seed was considered germinated when its radicle had perforated the integument. Germination capacity was estimated by the percentage of germination obtained 2 months after sowing. Calculation of relative germination adapted from Sharma (1973) (ratio of the germination capacity in the given experimental conditions to the germination capacity of the control sample) allowed for easy comparison among species.

Each experiment was repeated three times on 100 seeds. Variance analyses were completed after angular transformation of percentages. When F-values were significant ($P < 0.05$), means were compared by Newman–Keuls test with $P < 0.05$. Comparison of means in pairs was performed using Student's t-test with $P < 0.05$, the difference being significant if $t > 2.77$ (4 d.f.).

3. Results

Table 3 demonstrates that in the cases of *A. ataxacantha*, *A. dudgeoni*, *A. kamerunensis*, *A. senegal* and *A. ehrenbergiana*, germination capacity was identical whether seeds were scarified or not before sowing. For the remaining five species, germination capacity of intact seeds ranged between 19 and 39% but increased significantly with scarification (66–97%).

Table 3
Germination capacity (measured 2 months after sowing in Dakar) of intact seeds and seeds scarified by removal of a small piece of integument (Newman–Keuls test at $P < 0.05$ applied to each row)

Species	Germination capacity (%)	
	Intact seed	Scarified seed
A. ataxacantha	79.3 a	87.1 a
A. dudgeoni	53.3 a	61.0 a
A. kamerunensis	72.9 a	77.8 a
A. senegal	94.9 a	93.7 a
A. erhenbergiana	84.0 a	91.5 a
A. nilotica	16.1 b	66.5 a
A. raddiana	38.6 b	97.0 a
A. seyal	30.3 b	94.5 a
A. sieberiana	31.6 b	82.8 a
F. albida	35.0 b	92.5 a

Fig. 1 shows that seed survival in the different species varied according to fire intensity and seed position in relation to the soil. In all species, regardless of fire intensity, viability in buried seed (positions −5 and −2 cm) remained unchanged. The same applies for seeds placed 4.5 m above soil. When fire was of low intensity (100 g combustible m^{-2}), seed viability in the majority of species was reduced when they were placed on the soil (level 0) and 10 cm above. However, this loss in viability is only significant for *A. senegal* and *A. ehrenbergiana* (Fig. 1D and E). In the case of medium intensity fire, all the seeds of *A. ataxacantha* and *A. dudgeoni* placed less than 50 cm above the soil were destroyed (Fig. 1A and B). In contrast, where seeds of *A. nilotica* and *A. sieberiana* were concerned, a fraction of seeds always remained viable whatever their position (Fig. 1F and I). During high intensity fire (500 g combustible m^{-2}), seeds from all species placed at the lowest altitudes (0, 10, 50 cm) were charred. At 1.5 m, seed viability in *A. ataxacantha*, *A. dudgeoni*, *A. kamerunensis* and *A. erhenbergiana* was very poor (Fig. 1A–C and E), whereas that of *A. nilotica*, *A. seyal* and *A. sieberiana* did not differ significantly in relation to the control (relative germination close to 1) (Fig. 1F, H and I).

Fig. 2 shows that germination capacity of seeds after a non-lethal bush fire rarely differs from that of

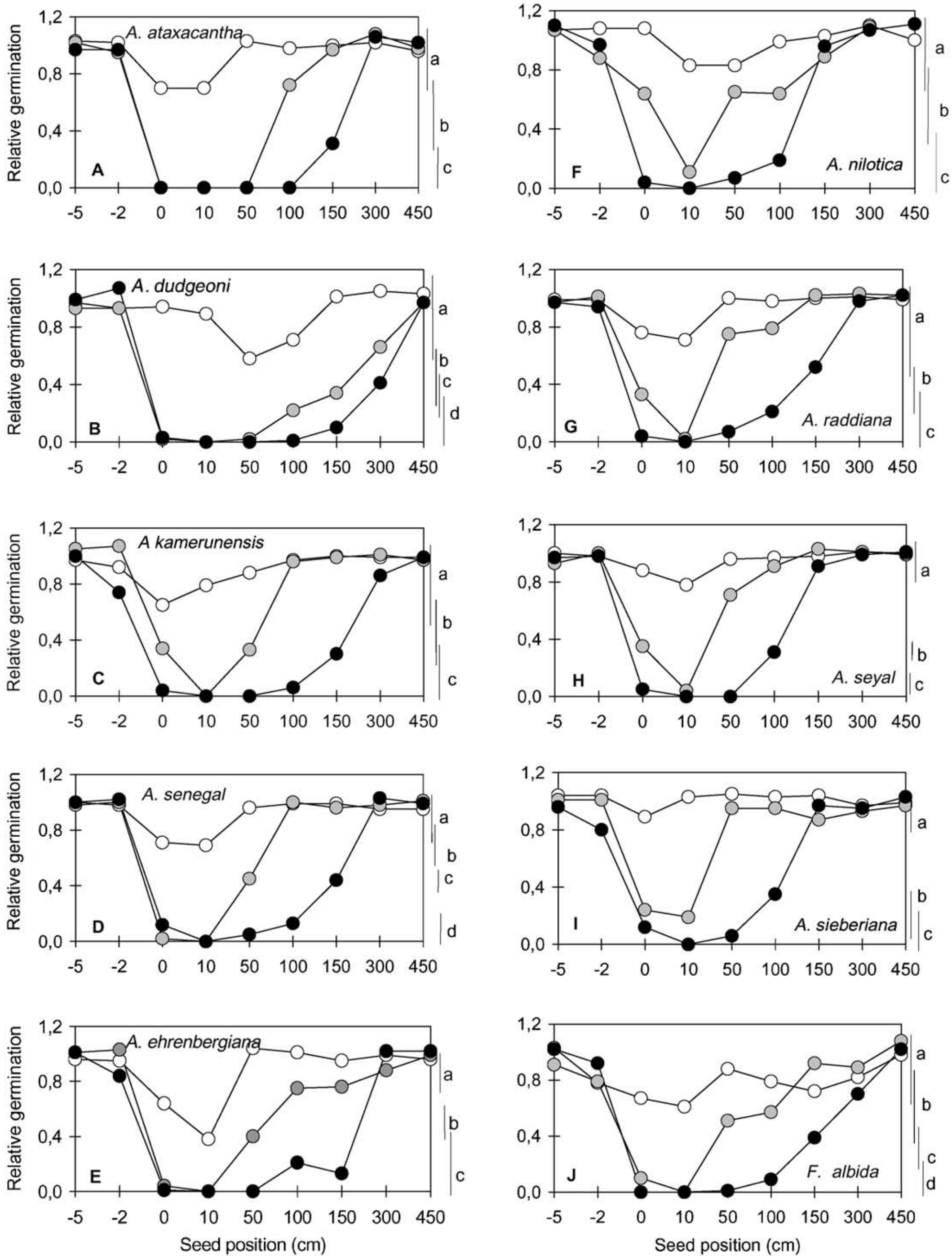

Fig. 1. Effect of seed position and fire intensity (low (in white), medium (in gray), high (in black)) on seed viability in different *Acacia* species (Newman–Keuls test at $P < 0.05$ for each species).

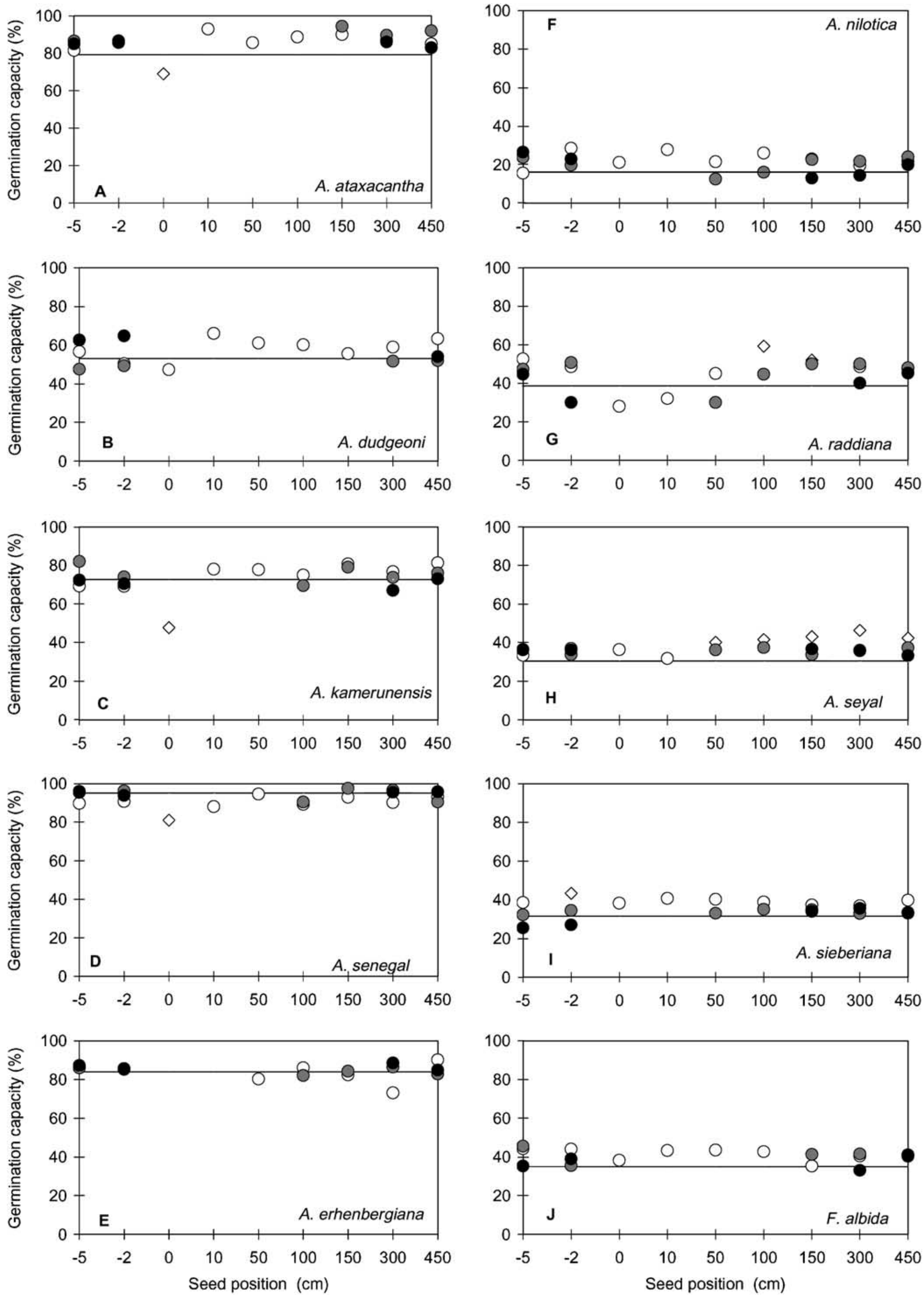

Fig. 2. Effect of seed position and fire intensity (low (in white), medium (in gray), high (in black)) on germination of acacia seed compared to non-scarified control (down stroke); a circle indicates that the difference with the control is not significant; a diamond indicates a significant difference (t-test, $P < 0.05$).

Table 4
Viability and germination capacity of seeds of *A. nilotica*, *A. sieberiana* and *F. albida* extracted from seed pods after high intensity fire (Newman–Keuls test at $P < 0.05$ applied to each column)

Seed position (cm)	Seed viability (%)			Germination capacity (%)		
	A. nilotica	*A. sieberiana*	*F. albida*	*A. nilotica*	*A. sieberiana*	*F. albida*
Control	67.1 a	78.3 a	94.8 a	16.1 a	31.6 a	35.0 a
−5	67.9 a	75.8 a	95.1 a	11.7 a	ND[a]	ND
−2	58.0 a	80.0 a	91.5 a	13.0 a	32.0 a	35.8 a
0	46.4 b	77.3 a	44.6 b	–	28.0 a	–
10	12.1 c	38.4 b	26.8 b	–	–	–
50	34.2 c	35.5 b	27.9 b	–	–	–
100	70.0 a	73.3 a	92.8 a	13.0 a	26.0 a	32.4 a
150	67.5 a	86.6 a	95.0 a	12.7 a	28.4 a	35.6 a
300	73.3 a	68.2 a	98 0 a	13.0 a	37.8 a	37.0 a
450	66.2 a	74.6 a	94.5 a	20.6 a	ND	34.0 a

[a] Not determined.

the control samples. This was the case for *A. ehrenbergiana*, *A. nilotica* and *F. albida* whatever the fire intensity and seed position (Fig. 2E, F and J). For *A. ataxacantha*, *A. kamerunensis* and *A. senegal*, the passage of low intensity fire on seeds placed on the surface of the soil caused a reduction in germination in relation to the control (Fig. 2A, C and D) which, in fact, corresponded to the loss of viability (non-significant) recorded in Fig. 1. The passage of low and medium intensity fire significantly improved germination for *A. raddiana* and *A. seyal* if the seeds were placed at varying positions between 50 and 450 cm (Fig. 2G and H). The seeds of *A. sieberiana* were the only ones that seemed to germinate better if they were buried (position −2 cm) during the passage of low intensity fire (Fig. 2I). It was also noted that for *A. nilotica*, *A. raddiana*, *A. seyal*, *A. sieberiana* and *F. albida*, germination capacities measured after the passage of fire remained significantly inferior to those obtained after mechanical scarification of seeds (Table 3).

Table 4 illustrates that the passage of high intensity fire never leads to complete seed destruction of *A. nilotica*, *A. sieberiana* and *F. albida* if they are contained within their seed pods. Their viability is, however, significantly depleted if their pods are located near ground level (0–50 cm). Of all the treatments that did not induce mortality in the seeds, none had a scarifying effect: germination capacity of extracted seeds never differed from that of the control samples.

4. Discussion

There have been numerous studies which have focused on the effect of fire or heat treatment on *Acacia* seed, either by altering the duration of exposure of seeds to a given temperature (Brown and Booysen, 1969; Portlock et al., 1990; Saharjo and Watanabe, 1997) or else by altering the position of seeds (burial) at the time of the passage of varying intensities of spreading fire (Omer, 1975; Auld, 1986; Pieterse and Caims, 1986; Sabiiti and Wein, 1987; Bradstock and Auld, 1995). These investigations made it possible to characterize three potential effects depending on the intensity of heat shock sustained by the seeds: none if the heat shock was too weak, seed destruction if the stress was too great and, finally, removal of integumental inhibition for intermediate stimuli. It must nevertheless be noted that the opportunities for heat shock to exercise a scarifying effect are sometimes very limited and some studies have concluded to a total absence of scarifying effect, as is the case, for example, for *A. constricta* (Cox et al., 1993) or *A. mangium* (Saharjo and Watanabe, 1997).

Our study indicates that this type of seed reaction to fire and heat shock is not applicable to all species tested because some do not exhibit integument inhibition, i.e. their seeds germinate without the need for scarification. This was the case for *A. ataxacantha*, *A. dudgeoni*, *A. kamerunensis*, *A. senegal* and *A. erhenbergiana.* Excepting the latter, these species belong to the sub-genus *Aculeiferum*, whilst species of the sub-genus *Acacia* exhibit integument dormancy which necessitates scarification prior to sowing in order to ensure rapid, synchronous germination. This observation confirms those of Danthu et al. (1992) and Masamba (1994) on the absence of integumental dormancy in *A. senegal*. It also explains sensitivity to fire of seeds belonging to this species as observed by Teketay (1996). The difference between the two sub-genera has already been indicated in relation to other criteria. In particular, Danthu et al. (1996) showed in their study into the effect of the passage of seed through the digestive tract of ruminants, that seeds of *A. senegal* are completely digested by gastric juices, whereas seed from various species of *Acacia* sub-genus are excreted intact. Likewise, Danthu et al. (1992) demonstrated that immersing seeds in boiling water, even momentarily, destroys seeds of *A. senegal*, whereas it neither hampers nor encourages germination of *F. albida* and *A. nilotica* (Brown and Booysen, 1969; Teketay, 1996). This difference in behavior derives from certain anatomical characteristics that distinguishes the seed and fruit of these two sub-genera. The sub-genus *Aculeiferum* is characterized by its dehiscent, chartaceous seed pod and its discoid seed, which are well adapted to wind born dissemination (Coe and Coe, 1987; Danthu et al., 1992; Vassal, 1975, 1998). Seed of *Acacia* and *F. albida* species have hard seed coats that induce high dormancy, pods which are generally fleshy and sometimes indehiscent, and are adapted to zoochory (Coe and Coe, 1987; Hauser, 1994; Diallo et al., 1996). This difference in the ability to survive after fire is probably due to the presence, in species of the *Acacia* sub-genus and *F. albida*, of a tegument that affords a greater degree of protection than that of *Aculeiferum*, even if from a histological point of view, there is no marked difference in the seed coat structure of the two groups of species (Vassal, 1975).

The protective effect exerted by the soil during the passage of spreading fire is well documented. It is dependent for the main part on a number factors: fire intensity, depth of seed burial, soil type and water content (Portlock et al., 1990; Bradstock and Auld, 1995; Saharjo and Watanabe, 1997). In Sahelian conditions (low or medium intensity fire passing over dry, sandy substrate), seed buried two or more centimeters beneath the soil are subject to low grade heat shock (temperature $< 60\,^{\circ}$C) which results in no mortality. This finding confirms earlier works of Brown and Booysen (1969), Auld and O'Connell (1991) and Bradstock and Auld (1995). Our results also demonstrate that with the exception of *A. sieberiana* in low intensity fire, none of the species experienced improved germination in these conditions. This observation can be compared to the conclusions of Auld and O'Connell (1991) regarding various Australian acacias and Saharjo and Watanabe (1997) in respect of *A. mangium* for which improved germination was achieved only after more radical treatment (raised temperature, longer duration). It does not contradict the findings of Oba (1990) and Bradstock and Auld (1995) which revealed that germination of *A. tortilis* and *A. suavolens* was stimulated during the passage of fire because of the estimated combustible biomass for these studies (65 and 6–20 t ha^{-1}, respectively). It would seem possible then to conclude that in Sahelian conditions, the passage of fire fed by combustible biomass close to 1 t ha^{-1} (Gillet, 1967) does not represent a stimulus which is sufficient to ensure the removal of seed coat inhibition of acacia seed buried in the soil.

Seed located in the canopy at the time of the passage fire (in the case of dehiscent pods) are generally destroyed if at low altitude. A greater degree of mortality is observed in the species of *Aculeiferum* sub-genus, they only survive if they are located at a height of $\geq$3 m, where they are subjected to heat shock of less than 100 °C, whereas seed of the *Acacia* sub-genus generally survive at 1.5 m with brief exposure to temperatures above 240 °C. In these conditions, the only seed to exhibit an increase in germination capacity after the passage of fire, and under a few experimental conditions only, was that of *A. raddiana* and *A. seyal*. This improvement in germination capacity is, however, very poor and remains significantly inferior to that observed after mechanical scarification.

Thus, for some species, particularly those belonging to the *Aculeiferum* sub-genus, absence of seed coat inhibition reduces the response to fire to two possible behaviors: seed viability preservation or seed mortality. For the other species (sub-genus *Acacia* and *F. albida*) which display tegumental inhibition, our study was not able to provide any obvious evidence of a scarifying effect by bush fire, regardless of whether seed was naked or contained in its pod. The only seed to show a significant, albeit slight, improvement of germination capacity, under a few experimental conditions, was that of *A. seyal*, *A. nilotica* and *A. sieberiana.* This behavior can be ascribed to the absence of scarifying effect noted for these species after passage through the digestive tract of various domestic ruminants (Danthu et al., 1996). This is further proof of the extreme hardiness of these seeds resulting from their adaptation to the prevailing ecological conditions in this dry zone (Gutterman, 1994).

It would thus seem possible to conclude that, contrary to what has been observed in Mediterranean ecosystems (Tarrega et al., 1992; Bradstock and Auld, 1995) and wet tropical zones (Oba, 1990), the passage of spreading fire is not a factor which induces germination in acacia seeds. This observation implies that in dry savannas, it is not feasible to consider fire as an accessory to reforestation or to the regeneration of acacia stands, as is the case for certain species of *Cistus* and Mediterranean *Pinus* (Trabaud and Oustric, 1989; Martínez-Sánchez et al., 1995). The increased regeneration of species after the passage of fire is more likely to be the result of a reduction in the number of competing plantlets than of any germinating inducing physiological alteration to seed (Gillon, 1983; Monnier, 1990).

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