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# Germination strategy of the East African savanna tree *Acacia tortilis*

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**Abstract:** Germination of *Acacia tortilis* seeds strongly depends on micro-site conditions. In Lake Manyara National Park, Tanzania, *Acacia tortilis* occurs abundantly in recently abandoned arable fields and in elephant-mediated gaps in acacia woodland, but does not regenerate in grass swards or beneath canopies. We examined the germination of *Acacia tortilis* using field and laboratory experiments. Seeds placed on top of the soil rarely germinated, while seeds covered with elephant dung or buried under the soil surface had a germination success between 23– 43%. On bare soil 39% of both the dung-covered and buried seeds germinated, in perennial grass swards 24–43%, and under tree canopies 10–24% respectively. In laboratory experiments, seed water absorption correlated positively with temperature up to 41 °C, while subsequent germination was optimal at lower (21–23 °C) temperatures. Seeds that had absorbed water lost their viability when kept above 35.5 °C. The absence of light did not significantly influence germination success. *Acacia tortilis* does not actively disperse its seeds, but regeneration outside tree canopies was substantial. The regeneration potential thus strongly depends on the physiognomy of the vegetation.

**Key Words:** fire, herbivores, rainfall, seed dispersal, seeds, Tanzania, vegetation, woodland dynamics

## INTRODUCTION

Acacia trees are key elements in African savannas. They provide food and shelter for mammals, birds (Or & Ward 2003) and insects (Krüger & McGavin 1998). People value the trees because they provide fodder for livestock (Reid & Ellis 1995), firewood and charcoal, gums and resins (Midgley & Bond 2001). The distribution patterns of these trees are governed by variations in soil characteristics (Scholes 1990), rainfall (Radford *et al.* 2001), fire (Bond *et al.* 2001) and herbivory (Bond & Loffell 2001, Bond *et al.* 2001). The spatio-temporal variability in acacia abundance may be explained by seed dispersal mechanisms and conditions that lead to successful establishment of seedlings. Seed dormancy (Skordilis & Thanos 1995) and seed dispersal (Miller 1994a,b) enable escape from unfavourable conditions. Indeed, the life histories of plant species have been subjected to selective forces that determine whether a young plant of a given species is at the right spot at the right time to develop into an adult. The central question in savanna dynamics is perhaps not so much what determines tree mortality, as what determines where new stands emerge.

In Lake Manyara National Park, Tanzania, adult *Acacia tortilis* (Forssk.) Hayne trees, the predominant *Acacia* species here, are mainly killed by elephant *Loxodonta africana* Blumenbach (Douglas-Hamilton 1972, Mwalyosi 1990); fire is virtually absent in the park. Acacia regeneration does not occur underneath the parent canopy (Mwalyosi 1990, Smith & Goodman 1986, Smith & Shackleton 1988, Vesey-FitzGerald 1973). Regeneration occurs in gaps in the woodland canopy, and especially on abandoned farms, added to the park in the early 1960s and in 1990.

The objective of this study is to determine whether this regeneration pattern of *A. tortilis* reflects the species' germination strategy. Field experiments were conducted to (1) establish under what conditions seeds germinate. Seed germination was monitored in three different vegetation types, with the position of the seeds being varied to simulate seeds in the soil seed bank, seeds excreted in dung, scattered seed on the soil surface, and seeds underneath an *A. tortilis* canopy. To study the

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physiological conditions that stimulate seed germination, we conducted laboratory experiments to establish (2) the effect of temperature and light on water imbibition and germination, and (3) the effect of temperature on seed survival. Furthermore, seeds were (4) subjected to dry heat treatments to simulate the effect of fire on germination.

## METHODS

### Study site and species

The field experiments were conducted at Ndala Research Camp (3°30′S, 35°45′E) in Lake Manyara National Park, northern Tanzania. The main area of the park is situated between Lake Manyara and the steeply rising escarpment of the Great Rift Valley. The park area at the foot of the escarpment consists of various lacustrine terraces and alluvial fans. The lakeshore, liable to flooding by the lake, is characterized by alkaline grasslands. Except where in the northern part of the park seepage sustains a broad-leaved forest dominated by *Trichilia emetica* Vahl, the lacustrine terraces, which are not flooded by the lake, are characterized by acacia woodlands, dominated by *A. tortilis* (Loth & Prins 1986). The mean annual rainfall is 650 mm, with a bimodal distribution pattern. The mean annual temperature is 21 °C, and the mean monthly temperatures do not deviate more than 3 °C from the yearly mean (Loth & Prins 1986).

*Acacia tortilis* (Forssk.) Hayne ssp. *spirocarpa* (A. Rich.) Brenan is a leguminous tree with an umbrella-shaped canopy. Canopies of mature trees may reach a diameter of over 30 m. After the main flowering period (May–July) the mature, indehiscent pods fall to the ground, where they can be found in large numbers between October–December. Unripe seed coats are green and soft, becoming brown and hard upon ripening.

Mature *Acacia tortilis* seeds were collected from freshly fallen pods at various locations in the park between September–November 1995, and undamaged seeds that did not show any markings on the seed coat, were retained for the experiments. Seeds collected throughout the entire period were pooled and stored in closed tins. To avoid losses of stored seeds to bruchid beetle (Bruchidae) infestation (Vir & Jindal 1994), the stored seeds were sprayed with a household insecticide (0.19% pyrethrum, 0.105% permethrin, 0.5% dichlorvos and 0.5% piperonyl butoxide).

### Field experiments

*Effect of parent tree on seed germination* (*parent tree study*). This experiment was aimed at separating the effect of allelopathic competition from that of lack of light on seed germination. The germination success of seeds placed under the canopies of *A. tortilis* (N = 20), *Gardenia ternifolia* Schum. & Thonn. (N = 8) trees, and under two shrub species, *Cadaba farinosa* Forssk. and *Acalypha fructicosa* Forssk. (N = 13 for the two species combined) was compared. The fraction of photosynthetically active radiation (PAR) reaching the soil surface at each location was measured using a line sensor (TFDL, Wageningen, The Netherlands), whereby the current reading in direct sunlight was used as the reference value. During the measurements the line sensor was directed perpendicular to the incoming sunlight. The measurements were carried out between 11h00 and 13h00. Under each canopy, two 3-cm-high PVC rings with a diameter of 10 cm were placed 1 cm deep into the soil. Twelve *Acacia* seeds (average seed weight of 320 fully developed seeds = 0.042 ± 0.007 g) were buried at 1 cm depth with regular spacing in each ring. This is well within the maximum emergence depth (9.5 cm; Bond *et al.* 1999). The experimental sites were screened off with chicken wire with 1.5-cm mesh to prevent seed predation. Every 4 d the number of emerging seeds as identified by the cracking of the soil surface and the number of newly emerged seedlings was recorded. The experiment started on 15 December 1995 and continued until 2 wk after the last rainfall event, on 26 May 1996. The experiment was rain fed, and rainfall was recorded daily at the research station.

*Effects of habitat type on seed germination* (*habitat type study*). The effects of habitat type and micro-site characteristics on *A. tortilis* seed germination were studied in a full factorial design. The experiment was carried out in duplicate in three different habitat types: bare soil without shading, within swards of the perennial grass *Cenchrus ciliaris* L., and under mature *A. tortilis* canopy with herbaceous undergrowth. Three treatments were applied to the seeds: seeds were placed on top of the soil, covered with a 5-cm-thick layer of elephant dung, or buried 1 cm deep in the soil. These treatments simulated scattered loose seeds on top of the soil, seeds excreted in elephant faeces, and seeds in the soil seed bank. Each experimental site consisted of nine PVC rings, 3 cm high, with a diameter of 10 cm. The treatments were randomly assigned to the rings in a Latin square design. Twelve seeds were placed in a regular pattern in each ring. Germinated seeds were scored as above. The experiment was rain fed and ran from 15 February to 16 May 1996.

*Effect of shading and wetting on soil temperature* (*shading/wetting study*). The effect of shading on soil temperature was measured in a 30-cm-tall PVC pipe with diameter of 9 cm filled with loamy sand, the predominant soil type (Loth & Prins 1986). One pipe was placed in full sun and another under a shade of gunny-sacking cloth, resulting in a 95% reduction in incoming radiation. On 45 d during a 3-mo period (1 June–11 August 1995) the temperature at 1 cm in the soil was measured at 2-h intervals at 07h00–21h00. On about every other day ($N = 25$) the soil was wetted in both treatments after the 17h00 temperature reading, and soil temperature measured again after 10 min.

### Laboratory experiments

The laboratory experiments were carried out at Wageningen University in 1997. The seeds were transported to the Netherlands in closed tins.

*Effect of temperature and light on seed water absorption rate and germination rate* (*temperature/light study*). The effect of temperature on water absorption and germination was experimentally assessed by placing six Petri dishes containing 20 seeds each at 17, 21, 25, 29, 33 and 41 °C under 12 h light/dark conditions in Weiss climate chambers. The effect of light at these temperatures was investigated by covering six additional Petri dishes with 20 seeds each with aluminium trays. The Petri dishes had permanent moist tissue on the bottom. The relative humidity was kept at 80%. The numbers of swollen seeds as a consequence of water absorption and germinating seeds were scored daily on weekdays for a period of 60 d (17, 25 and 33 °C), 38 d (21 and 29 °C) and 12 d (41 °C). The duration at 41 °C was limited, because none of the seeds germinated; all became moulded after only a few days. Seeds were considered to have germinated when the radicle was clearly visible. Swollen seeds that had not germinated but had been covered with fungi for at least 5 d were considered lost. This was confirmed afterwards by evaluating the viability of embryos of such seeds, following Moore 1973. Swollen seeds and germinating seeds were removed from the seed coat to determine whether the seeds had been infested with bruchid larvae.

*Determination of optimal germination temperature of imbibed seeds* (*optimal temperature study*). The effect of temperature on the germination rate was determined in seeds that, after treatment, had absorbed water within 24 h. The treatment consisted of immersing the seeds in hot water (80 °C), which was allowed to cool, and soaking the seeds for 24 h (Mbuya *et al.* 1994). Seeds that had absorbed water after 24 h were divided over five (17, 25 and 33 °C), six (21, 29 and 41 °C) and eight (11 °C) Petri dishes with moist tissue on the bottom. The number of germinated seeds was counted for 8 d, every 12 h during the first 2 d and daily thereafter.

*Effect of dry heat on water absorption and germination* (*dry heat study*). For the determination of the effect of dry heat on seed germination, those seeds were used which had not swollen after 60 d at 17, 25 or 33 °C. Air-dried seeds were either placed in Petri dishes with moist tissue on the bottom, or after being put for 15 s in an oven kept at 150, 300 and 450 °C. For each temperature treatment, six batches of 20 seeds were prepared by placing 10 seeds in ceramic cups in the oven; and allowed to cool down. For the treatment at 450 °C, the ceramic cups were filled with fine sand, and the seeds placed on top of the sand, after it appeared, during an earlier attempt, that several seeds attained burn marks. The number of swollen and germinated seeds at 29 °C was scored daily for 12 d.

### Data analysis

Bonferroni multiple comparison tests were carried out to detect differences among means. In the experiment where the effects of habitat type on seed germination was tested, two-way ANOVA of arcsine-transformed data showed that there was no block effect ($F_{1,36} = 1.90$, $P > 0.1$), so the replicates were lumped. The germination success at the end of the experiment was determined by analysis of covariance, with site and treatment of the seeds as categorical variables, and time as covariate.

A number of swollen and germinated seeds in the laboratory experiments appeared to have been infested by bruchid larvae. These seeds were excluded from the analyses. The data were transformed when the variances were not homogeneous. Proportional data were arcsine transformed.

Seed germination success in the second field experiment and in the laboratory were analysed using a multiple logistic regression. If a seed has absorbed water or germinated, it is considered transmuted (transmuted seed: status 1; untransmuted: status 0). The proportion of transmuted seeds, p, is related to time (t), humidity (R) and temperature (T) and their interactions. A predictor for proportional data is provided by the logit transformation of p: $\ln(p/(1-p)) = b_0 + b_1 \times t + b_2 \times t^2 + b_3 \times R + b_4 \times R^2 + b_5 \times t \times R + b_6 \times T + b_7 \times T^2 + b_8 \times t \times T + b_9 \times R \times T$ (Sokal & Rohlf 1995, ter Braak & Looman 1995); treatments and their interactions were entered as categorical variables. We analysed the data for the cumulative proportion of transmuted seeds only. Squared terms were also included in the model, because optimum responses were expected. Second order interaction terms were included to account for tractable interactions among the variables. The best fit for the logistic regression was obtained by including those parameters in the model that minimized the deviance, described by the statistic $-2LL$, where $LL$ stands for the $\log_e$ of the likelihood (Huisman *et al.* 1993, ter Braak & Looman 1995). Multiple logistic regressions were carried out with SPSS (SPSS Inc. 2001).

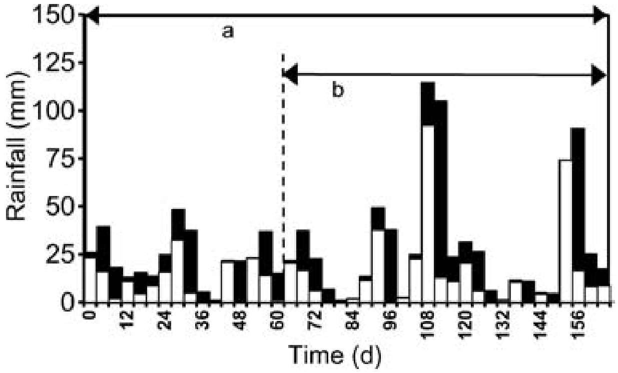

**Figure 1.** Rainfall totals from 15 December 1995 (Day = 0, start of field experiment 1) until 27 May (D = 164), the last interval in which rainfall was recorded. Light bars: 4-d totals, black bars: 8-d totals, a = field experiment 1, b = field experiment 2.

In the habitat type study the total amount of rainfall recorded during the preceding 4 or 8 d was used as an indicator for humidity, and the mean $T_{max}$ over the preceding 4 d as an indicator for temperature.

The effects of temperature and light treatment on loss of imbibed seeds through moulding in the temperature/light study were examined for each Petri dish (N = 54) at the temperature range from 17 to 33 °C. For each Petri dish the number of lost seeds within 35 d was scored and calculated as the percentage of swollen seeds that had not been infested by bruchid larvae. The results of the treatment at 41 °C were omitted, because all swollen seeds were lost after only a few days. We applied an analysis of variance here, with light treatment as categorical variable and temperature as covariate, rather than logistic regression analysis, because seed loss could not be related to the day on which the seeds had absorbed water.

The optimum germination temperature in the dry heat study was established by plotting the half-time values, i.e. the number of hours required for half of the seeds of the total number of germinated seeds to have germinated within an 8-d period, against temperature, fitted with a second-order polynomial curve.

## RESULTS

*Field experiments.* The rainfall amounts recorded in 4- and 8-d intervals are provided in Figure 1.

*Parent tree study.* The fraction of PAR reaching the ground did not differ between the two tree species ($P > 0.05$), but underneath shrubs less light was intercepted by the canopy (shrub: 0.84, *Acacia*: 0.93, and *Gardenia*: 0.94; $F_{2,39} = 8.59$, $P < 0.001$). The proportion of the seeds that germinated was not significantly different whether planted under trees or under shrubs, and the proportion of germinated seeds did not depend on the amount of light reaching the soil ($F_{3,78} = 0.64$, $P > 0.1$).

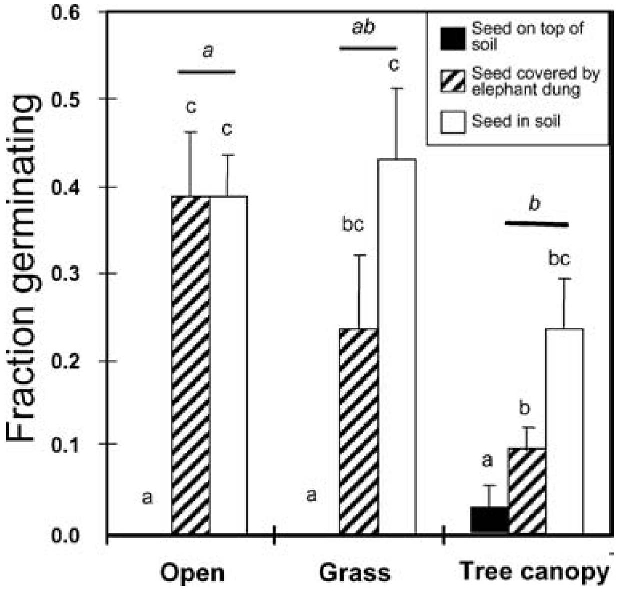

**Figure 2.** *Acacia tortilis* seed germination in open sites, in perennial grass sward and under *Acacia* canopy with different seed treatments. Means are calculated for 18 plots per treatment, with 12 seeds each. Bars indicate 95% confidence limit. Letters denote significant differences at $\alpha = 0.05$ for all treatments, italic letters for buried and dung-covered seeds combined.

*Habitat type study.* In grass swards and under acacia canopies ~65% (N = 34) and > 90% (N = 40) of PAR was intercepted. The main effects, site ($F_{2,45} = 4.19$, $P < 0.05$), treatment ($F_{2,45} = 51.8$, $P < 0.001$), and their interaction ($F_{4,45} = 2.95$, $P < 0.05$) had a significant effect on germination success. One-way ANOVA of the grouped variates showed that seeds placed on top of the soil had significantly lower germination success than the other treatments (Figure 2). All seeds placed on top of the soil failed to germinate except for two seeds in one single ring underneath acacia canopy. When seeds placed on top of the soil were omitted from the analysis, there was no significant difference in germination success between buried seeds and seeds covered by elephant dung ($F_{1,34} = 3.30$, $P > 0.05$). Seeds under canopies had a significantly lower germination success than seeds placed in the other sites ($F_{2,33} = 5.51$, $P < 0.01$); the interaction term was no longer significant.

The logistic regression analyses were carried out with omission of those cases where seeds were placed on top of the soil. The model based on cumulative rainfall over the past 8 d (Figure 1) and mean $T_{max}$ over the preceding 4 d provided the best fit ($R^2 = 0.22$, Table 1). The probability that seeds germinated was highest following a wet period (total amount of rainfall in an 8-d period > 100 mm), but

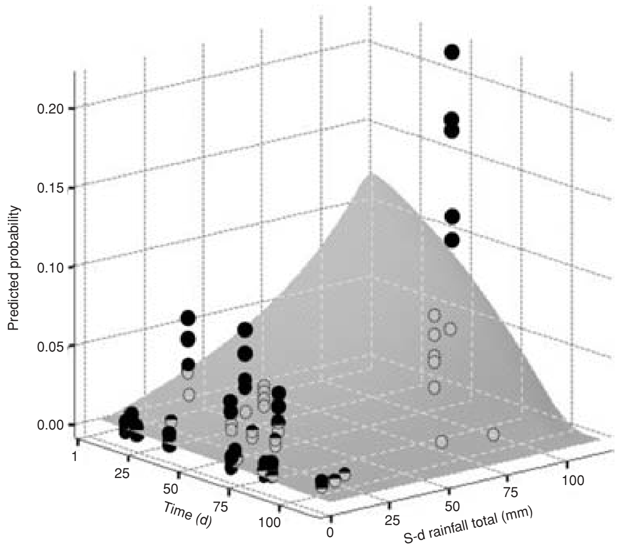

**Figure 3.** Germination probability of *Acacia tortilis* seeds in the field as a function of time and rainfall (8-d totals), as determined by multiple logistic regression model 4 in Table 1. Data smoothing for all data used normal kernel (SPSS 2001) with multiplier 1 for time and 2 for rainfall totals. Differences in habitat type and position of the seeds are not separately indicated.

germination dropped to nearly 0 in subsequent periods with the second-highest amounts of rainfall (Figure 3).

*Shading/wetting study.* The mean dry soil temperature in the full sun and in the shade between 11h00 and 17h00 was 33.6 ± 0.77 °C and 25.2 ± 0.38 °C (N = 180) respectively. The highest temperatures and the greatest differences were measured at 15h00 ($T_{sun} = 37.8 \pm 5.2$ °C; $T_{shade} = 27.2 \pm 1.9$ °C). At 07h00 the mean soil temperature in both treatments was equal (17.2 °C with 95% confidence interval of 1.03 and 0.75 °C for sun and shade respectively). The drop in temperature after soil wetting was linearly dependent on the soil temperature before wetting ($T_{wet} = 0.41 \times T_{dry} + 12.3$; $F_{1,47} = 85.9$, $P < 0.001$, $R^2 = 0.64$).

## Laboratory experiments

*Temperature/light study.* At all temperatures more than half of those seeds that absorbed water did so during the first 10 d (Figure 4a). At 41 °C the water absorption rate was highest, but none of these seeds germinated (Figure 4b). Inclusion of light treatment in the logistic regression analysis for water absorption did not significantly improve the model ($\chi^2 = 0.17$, df = 1, $P > 0.1$). Both the number of days and the temperature at which the seeds were kept during the experiment had a significant effect on the water absorption probability ($\chi^2 = 717$, df = 2, $P < 0.001$), but not the interaction term ($\chi^2 = 1.84$, df = 1, $P > 0.1$). Inclusion of a quadratic temperature term significantly decreased the deviance ($\chi^2 = 68.9$, df = 1, $P < 0.001$). Consequently, the model predicts that some seeds absorb water immediately after the seeds have been placed in a moist environment, while the probability, $p_s$, that the remaining seeds absorb water declines with time: $p_s = 1/(1 + \exp(1.57 + 0.064 \times D + 0.168 \times T - 0.0038 \times T^2))$, where D is number of days and T is temperature in °C (see Figure 5a). Above 25 °C the water absorption rate increased exponentially with temperature. The presence or absence of light did not have a significant effect on seed germination. Time did not have a significant effect on the probability of seed germination, $p_g$, per se, but the interactions of time with temperature and the squared temperature were significant (both terms $P < 0.001$), resulting in a decrease in the probability of remaining seeds to germinate with time ($p_g = 1/(1 + \exp(6.55 - 0.292 \times T + 0.0069 \times T^2 + 0.0074 \times D \times T - 0.0002 \times D \times T^2))$; Figure 5b). The logistic regression model for seed germination predicts that the optimum temperature for seed germination is 21 °C.

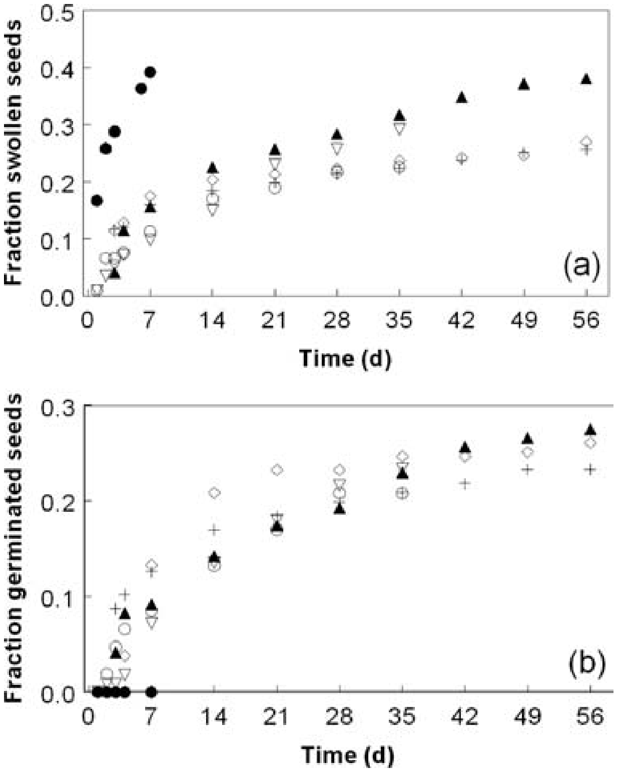

**Figure 4.** Daily and weekly cumulative fraction of *Acacia tortilis* seeds, kept in the laboratory at different constant temperatures that had absorbed water ('*swollen*'; a), or had germinated (b). The results of the germination experiments carried out under 12-hourly light/dark and continuous dark conditions were combined. The fractions have been corrected for seeds that were infested by bruchid beetles. ◇ seeds kept at 17 °C, ○: 21 °C, +: 25 °C, ▽: 29 °C; ▲ 33 °C, ●: 41 °C.

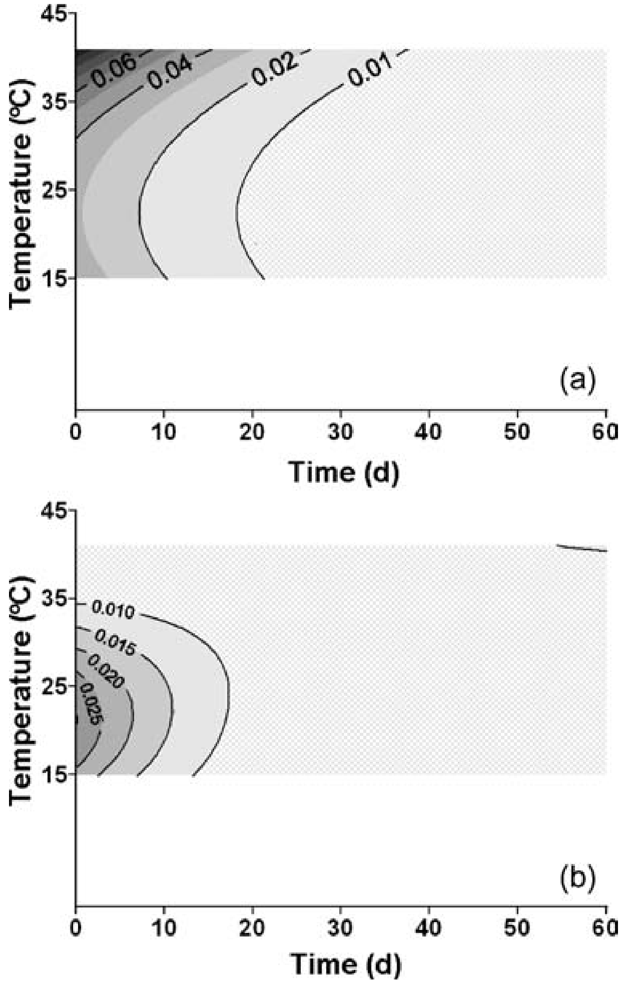

**Figure 5.** Probabilities that (a) *Acacia tortilis* seeds from a seed lot swell due to water aborption, or that (b) swollen seeds germinate at different temperatures in laboratory experiments.

*Optimal temperature study.* Most seeds that had swollen after immersion in hot water germinated between 17 and 25 °C, with an optimum temperature of 22.4 °C as derived from the fitted polynomial curve ($y = -1.46 + 0.208s - 0.00471s^2$; $R^2 = 0.82$; Figure 6). The model predicts that no seeds germinate at temperatures below 8.7 or above 35.5 °C.

*Dry heat study.* Seeds that had not absorbed water after being placed in a wet environment for 60 d did so after a short exposure to dry heat. The difference in germination success between similar seeds not exposed to dry heat and those exposed to dry heat ≥ 300 °C was significant ($F_{3,20} = 7.44$, $P < 0.01$; Table 1). At the highest temperature, a quarter of the seeds that absorbed water, were killed, while at the other temperatures and in the control almost none of the swollen seeds lost their viability; the effect of heat on seed mortality at temperatures lower than 450 °C was not significant ($F_{3,15} = 2.26$, $P > 0.1$).

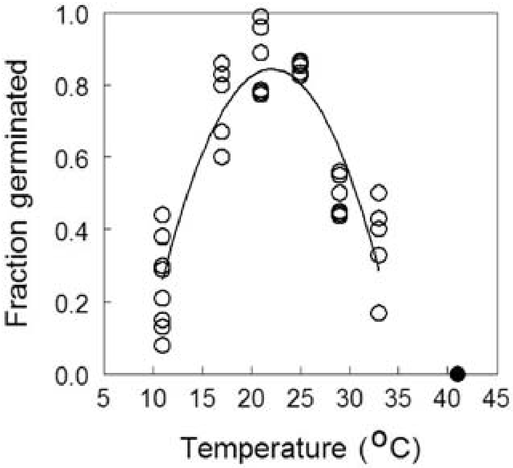

**Figure 6.** Proportion of imbibed *Acacia tortilis* seeds in the laboratory that germinated at different temperatures within an 8-d period. Fitted curve excluded complete failure of seeds to germinate at 41 °C (black dot).

## DISCUSSION

Acacia seed germination requires a moist environment and favourable temperatures, but the response to both moisture and temperature is not a simple optimal one. In contrast to the findings of Choinsky & Tuohy (1991), our results suggest that *A. tortilis* seeds germinate better at sites with a considerable temperature amplitude. At temperatures above 25 °C the water absorption rate of

**Table 1.** Comparison of goodness-of-fit of logistic regression models (the −2LL log-likelihood statistic, analogous to the error sum of squares in linear regression, and the $R^2$) for the germination of *Acacia tortilis* seeds, where in three different habitat types seeds were placed in different positions. C = constant; $R_4$, $R_8$ = Total rainfall over preceding period of respectively 4 and 8 d; D = number of days since start of experiment; T = mean maximum temperature between observations (4 d). In all models the categorical variables (three habitat types and two positions of the seeds (seeds placed on top of the soil omitted because only in one case seed germinated; see Figure 2)) and their interaction were also entered in the models (not shown in table).

| Nr | Model | − 2LL | $R^2$ |
|---|---|---|---|
| 1 | $C + axR_4 + bxD + cxD^2 + dxR_4xD + exR_4xD^2$ | 1133 | 0.15 |
| 2 | $C + axR_8 + bxD + cxD^2 + dxR_8xD + exR_8xD^2$ | 1061 | 0.21 |
| 3 | $C + axR_4 + bxT + cxT^2 + dxR_4xT + exR_4xT^2$ | 1192 | 0.10 |
| 4 | $C + axR_8 + bxT + cxT^2 + dxR_8xT + exR_8xT^2$ | 1044 | 0.22 |
| 5 | $C + axR_4 + bxD + cxD^2 + dxR_4xD$ | 1133 | 0.15 |
| 6 | $C + axR_8 + bxT + cxT^2 + dxR_8xT$ | 1061 | 0.21 |
| 7 | $C + axR_4 + bxT + cxT^2 + dxR_4xT$ | 1190 | 0.11 |
| 8 | $C + axR_8 + bxT + cxT^2 + dxR_8xT$ | 1109 | 0.17 |

the seeds increases exponentially (Figure 4a), while after imbibition lower temperatures enhance germination. Such situations are found close to the surface of exposed soils, where temperature fluctuations are highest. Uncovered, sun-exposed seeds dry out quickly in the field and die, but soil- or dung-covered seeds both germinate readily (parent tree study, Figure 2). A small amount of vegetation cover likely enhances the availability of seed available moisture, but does not seem to greatly reduce temperatures (Singh *et al.* 2004).

The germination success of seeds in suitably moist environments is therefore expected to be highest in sites well away from tree cover, and to decrease with increasing vegetation cover. This conclusion seems to contradict Smith & Shackleton (1988), who found that the relative frequency of newly germinated seedlings is higher under canopies than in open areas. This was the reverse for established (= 1-y old) seedlings. We feel that their outcome probably reflected the higher density of seeds in soil seed banks under *Acacia* canopies than in the open (*cf.* Argaw *et al.* 1999). The prolific germination and subsequent establishment of *A. tortilis* on freshly ploughed and recently abandoned fields (PL *pers. obs.*) can thus be the result of increased soil temperatures caused by tillage (Hayward *et al.* 1980, Lal 1986, Saran 1973). The large time window of several months (Figure 3) during which seeds can germinate, contributes to seedling survival in an environment where rainfall is a stochastic event (Figure 1).

Germination of *A. tortilis* seeds in the shade of trees is not optimal, regardless of cover species, and therefore seeds must be transported away from the parent canopy. *Acacia tortilis*, however, lacks an active seed dispersal mechanism. Dudley (1999) found that elephants ingested large amounts of *A. erioloba*, and dispersed the seeds over large distances. Ingestion by herbivores thus may result in the desired distribution, while dung provides the required water-holding environment necessary for germination (Miller 1996; this study). The hard seed coat prevents destruction of the seed during the mastication process (Coe & Coe 1987, Miller 1994a, Or & Ward 2003). Although most studies concluded that seed ingestion by herbivores increased germination success, Or & Ward also reported contrasting outcomes. We did not find differences in germination success after a 27-wk germination experiment carried out in the field with 6 and 30 batches of 20 seeds from pods and dung respectively (42.1% and 34.6% of seeds germinated; $F_{1,34} = 2.22$, $P > 0.05$). We favour the explanation offered by Miller (1994a,b) and Miller & Coe (1993), who suggested that ingestion of seeds by large herbivores reduces bruchid infestation of seeds. Dispersal from the parent tree prevents further infestation. The results from this study show that, for optimal germination, the seeds should be deposited by herbivores on bare spots.

Seed germination of many hard-coated legume seeds is stimulated by fire, and this study confirms that *A. tortilis* reacts similarly. In agreement with Dell (1980), it was found that treatment of impermeable seeds with dry heat caused such seeds to absorb water and germinate. Temperatures recorded in savanna fires at the soil surface may vary greatly, ranging from less than 70 °C to above 800 °C. Due to the low thermal conductivity of soil, temperatures at 2 cm below the soil surface seldom exceed 35 °C (reviewed in Frost & Robertson 1987, van de Vijver 1999, Singh *et al.* 2004). Seeds scattered on top of the soil are more likely to escape the heat of fires in small cracks and other soil roughness. We observed that *Acacia* regeneration was high on bare places where trees had died over the past 20 y. Presumably due to the high herbivore density, perennial grasses had not colonized gaps in the *Acacia* canopy rapidly; the herbivore density in Manyara is one of the highest in Africa (Prins & Beekman 1989). It is conceivable that *Acacia* seeds from which regeneration resulted were either transported there by herbivores, or existed on the spots vacated by the parent trees (*cf.* Argaw *et al.* 1999).

Midgley & Bond (2001) provided a comprehensive review of the demography of acacias. The findings of this study add to its understanding at the germination stage. We hypothesize that *Acacia* seed germination depends on the state of the vegetation (Figure 7). The transition of unsuitable *Acacia* canopies to potentially suitable, exposed sites is effected by elephant impact, or by senescence of the trees; fire has not occurred in the Park since 1958. Perennial grasses may colonize gaps, or gaps may remain bare for a longer period, mediated by a variable grazing pressure (Teague *et al.* 2004), and transitions to shrub and woodland may occur with species that are adapted to germinate under shaded conditions. Localized transitions from grasslands to bare soil can be brought about by animal activities (Teague *et al.* 2004). We found seed germination of *Acacia* in elephant dung deposited in closed-sward *Urochloa mosambicensis* (Hack.) Dandy grasslands, although establishment of *Acacia* in these grasslands was rare over a 40-y period, as could be concluded from inspection of a series of aerial photographs made in 1953, 1958, 1976, 1988 and 1996 (unpubl. data). The creation of temporary open gaps in grass swards by dung patches as reported by Brown & Archer (1987), although rare, may thus enhance germination from seeds in dung.

We conclude that *Acacia tortilis* regeneration optimally occurs in open, suitably moist conditions with large temperature fluctuations. Water absorption by seeds is best at high temperatures, while subsequent germination is optimal at lower temperatures. The availability of light influences neither water absorption by the seeds, nor germination. Furthermore, a dry heat treatment does break seed dormancy, suggesting that fire may enhance the

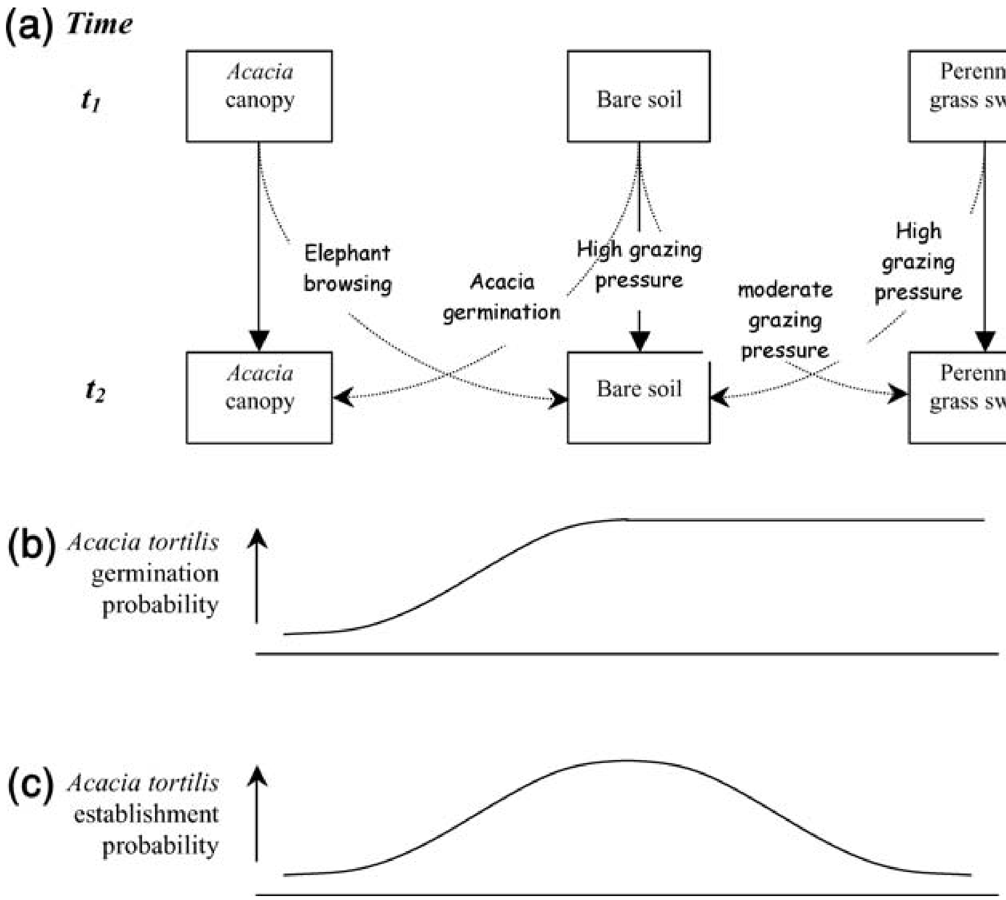

**Figure 7.** Vegetation states and transitions (a) in an East African savanna in the absence of fire. Transitions are indicated by dotted lines. *Acacia* canopy reverts to bare soil due to senescence of the trees or death caused by elephants. Under heavy grazing pressure, states may remain permanent (bare soil), or may change from perennial grass sward to bare soil. Under moderate grazing pressure, bare soil may change to perennial grass sward, and perennial grass swards may remain permanent, or may be invaded by woody species (not indicated in figure). *Acacia tortilis* seeds germinate poorly under tree canopies, but equally well in bare soil patches and grasslands (b). Seedling establishment is poor under tree canopies and in grasslands, but better in bare soil (c).

germination of *A. tortilis*. When fire is absent (Figure 7), the regeneration potential strongly depends on the physiognomy of the vegetation. Herbivores may transport seeds away from underneath *Acacia* canopies towards bare soil or grassland patches, enhancing the germination probability. Germinated seeds likely establish better in open areas.

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