Fire Suppression as Well as Seed Dispersal Play Critical Role in the Establishment of Forest Tree Species in Tropical Woodland

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Research Article

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Abstract

This study examined the mechanisms of facilitation and importance of seed dispersal during establishment of forest tree species in a tropical woodland. Seedling survival of *Syzygium guineense* ssp. *afromontanum* seedling (forest tree species) was monitored for 2.5 years in four different microsites in savannah-woodland in Malawi under *Ficus natalensis* (a potential nurse plant), *Brachystegia floribunda* (a woodland tree), and *Uapaca kirkiana* (a woodland tree), and in a treeless site. *S. guineense* ssp. *afromontanum* seed deposition was also monitored in the four sites, and the natural establishment of forest tree species was observed to confirm the importance of seed dispersal. Protection from fire was found to be the most important facilitation mechanism in this area, with a total fire-induced mortality rate of 43%. However, the rate was comparatively low under *F. natalensis*, where fire is thought to be inhibited due to the lack of light-demanding C4 grasses. *B. floribunda* also offered protection from fire, and seedling survival did not differ between these two microsites. However, only a few individual forest tree species naturally established under *B. floribunda*, indicating that the facilitative mechanism of fire suppression is not the only factor affecting establishment in this tropical woodland. A higher rate of seed dispersal was also observed under *F. natalensis* compared with the other three microsites, suggesting that dispersal processes are also critical for the establishment of forest tree species in woodland in this region.

Highlights

- Facilitation allowed forest tree species to establish in a tropical woodland.
- Fire suppression was an important mechanism of the facilitation there.
- Additionally, seed dispersal was an essential process for the establishment.

Introduction

Tropical forest and savannah-woodlands are major terrestrial biomes in tropical landscapes¹. Although their global occurrence is controlled by climate, on a regional to local scale, these two contrasting vegetation types occur within identical climatic conditions^{2,3}. Recent studies have reported the expansion of tropical forests into adjacent savannah-woodland in many parts of the world^{4,5,6,7}. These expansions depend on successful establishment of forest tree species because many constraints limit the establishment of forest tree species in savannah-woodland. For this reason, more emphasis has been placed on the importance of plant-plant interactions (i.e., facilitation) during the recruitment of forest tree species in savannah-woodland^{8,9,10,11,12,13}. Facilitation has been shown to exert both a direct and indirect effect on establishment through the modification of abiotic and biotic conditions by particular plants, so-called nurse plants^{14,15}. Although facilitation seems to play a prominent role, little is known about its precise mechanisms.

Previous studies suggest that seedling abundance and the survival of forest tree species under nurse plants is higher than in treeless areas of savannah-woodland^{8,9,10}. These studies further suggest that the facilitative effects, such as amelioration of water stress, act by suppressing the occurrence of fire and improving soil properties. However, the specific mechanisms remain unknown, partly because studies on the relative importance of the different factors affecting seedling survival are limited.

In addition to the facilitative effect on seedling survival, seed dispersal is thought to be critical for the recruitment of forest tree species in savannah-woodland. Indeed, if seeds of forest tree species are not dispersed, facilitation of seedling survival becomes secondary. However, most studies on the establishment of forest tree species in savannah-woodland tend to concentrate on post-seed dispersal stages^{10,16,17,18,19} with few having quantitatively demonstrated the importance of seed dispersal itself.

This study attempted to clarify the specific mechanisms of facilitation as well as the importance of seed dispersal during recruitment of forest tree species in a tropical woodland in northern Malawi, Southeastern Africa. *Ficus natalensis* (Moraceae) was included as a nurse plant because trees in this genus are widely known to play a role in establishment of tropical savannah-woodlands and post-agricultural sites^{20,21}. In some cases, *Ficus* trees drive the creation of forest patches, called “nucleation”²². In northern Malawi, the circular forest patches often occur within woodlands, with large fleshy fruit trees, such as *Ficus natalensis*, existing in the center²³. These structures are a general feature of “nucleated forest patches” rather than fragmented forests^{5,24}.

To clarify the specific mechanisms of facilitation, this study observed seedling survival of *Syzygium guineense* ssp. *afromontanum* (a common forest tree species) under *F. natalensis*, and in three other microsites for 2.5 years. The most notable cause of seedling mortality was recorded to determine the relative importance of different factors. In addition, seed rain of *S. guineense* ssp. *afromontanum* in the four microsites was monitored to determine the importance of seed dispersal processes in the recruitment of forest tree species. Natural seedling establishment of forest tree species was also observed to further confirm the importance of dispersal processes. Overall, this study aimed to determine the following: (1) the most important facilitative mechanism affecting seedling survival, and (2) the effect of seed dispersal on the establishment of forest tree species in tropical woodland.

Materials And Methods

Study area

This study was conducted in northern Malawi in Southeastern Africa, where tropical woodland, known as miombo woodland, covers approximately 2.7 million km². Miombo woodland is composed of three closely related genera of Caesalpiniaceae: *Brachystegia*, *Julbernardia*, and *Isoberlinia*²⁵. These are largely deciduous trees that reach up to canopy height of 10-20 m with continuous C4 grass layer. Montane rainforests also occur in this region on mountain crests and in valleys²⁶ and in contrast, are composed of evergreen trees with a tall canopy (20-25 m) and numerous lianas.

The study site (10°58'S, 34°04'E) was situated in a local zone governed by a rural village on the north Vipya Plateau. Mean annual precipitation is more than 1,200 mm on the north Vipya Plateau²⁷. Miombo woodland is predominant in the area but some montane rainforests also occur on mountain crests (> 1,800 m asl) and in valleys. Besides, circular forest patches (~10-1,800 m²; hereafter referred to as forest patches) composed of montane rainforest tree species are also found within the miombo woodland (1,700–1,800 m asl; Fujita, 2014). In this study site, miombo woodland is burnt by locals during late dry season (September to December) approximately every 2-3 years. Fire rarely spread far into the montane rainforest due to its closed canopy, lack of grass species and humid understory²⁸. Antelopes such as the common duiker (*Sylvicapra grimmia*) are found grazing in the study site. Local people rarely cut trees from the miombo woodlands and montane rainforests because of their location far from settlements.

Focal forest species

S. guineense ssp. *afromontanum* F. White (Myrtaceae) was used to monitor seedling survival and seed deposition. *S. guineense* ssp. *afromontanum* is endemic tree species of montane rainforests, and also commonly found on the Vipya Plateau²⁶. In the study area, *S. guineense* ssp. *afromontanum* is commonly found in forest patches within the miombo woodland. It is an evergreen tree that reaches heights of 30 m, and bears purple berries (fruit size = 1.6 × 1.4 cm, seed size = 1.2 × 1.1 cm, n = 6) during the rainy season (January to March).

Characteristics of the studied microsites in the miombo woodland

Four microsites were established in the miombo woodland as follows: 1) under *F. natalensis*, 2) under *Brachystegia floribunda*, 3) under *Uapaca kirkiana*, and 4) in treeless sites. *F. natalensis* (Moraceae) is a deciduous tree that reaches heights of 20 m. It occurs primarily in miombo woodland in the region, but is also found in the center of circular forest patches. It has two periods of ripening (August to October and January to April), and produces yellow-red syconia (1.1 × 1.0 cm, n = 10). *B. floribunda* (Caesalpinioideae) is deciduous and reaches heights of 20 m. It is a dominant tree species in the miombo woodlands producing pods from October to January. *U. kirkiana* (Phyllanthaceae) is a smaller tree of up to 13 m and is also common species in miombo woodland. It bears fleshy fruit (2.6 × 2.6 cm, n = 7) from September to December. The treeless sites consisted of areas in which there were no trees with crowns exceeding a 3-m radius or with a diameter at breast height (dbh) of > 5 cm.

Eight individual *F. natalensis* trees > 50 m from montane rainforest or forest patches were selected. The mean distance between the *F. natalensis* trees and forest or forest patches was 169 m (range = 56–307 m). *B. floribunda*, *U. kirkiana* and treeless sites were then established within 50 m of each *F. natalensis*. Individual *B. floribunda* and *U. kirkiana* trees with a height and dbh similar to those of the selected *F. natalensis* were chosen. *F. natalensis*, *B. floribunda* and *U. kirkiana* have little to no canopy overlap with other trees.

Originally, ten individual replicates were selected. But, two of the 10 replicates were destroyed by locals during the seedling survival and seed rain monitoring (see below); thus, the results of seed rain and

seedling survival were obtained from eight replicates per microsite and the results of environmental variables were calculated from ten replicates (see below).

Data collection

Environmental variables

Canopy openness and the percentage of grass cover were examined in each of the four microsites. To determine canopy cover, four hemispherical canopy photographs were obtained from each microsite during the rainy season (February 2012), after the leaves had fully expanded. Photographs were taken at the mid-point of the crown radius from the trunk or 1 m from the center of the treeless sites in each cardinal direction, at a 1-m height aboveground with a fish-eye lens (Raynox DCR-CF). They were then analyzed using Gap Light Analyzer software²⁹ to calculate canopy openness. The percentage of grass cover was estimated visually in four 1 × 1-m quadrats during the dry season (September 2012) before any fires occurred in the same locations as the canopy photographs were obtained.

S. guineense ssp. *afromontanum* seedling survival and causes of mortality

Seeds of *S. guineense* ssp. *afromontanum* were sown in a nursery in January 2012. Four weeks later after the sowing, the seedlings were then transplanted in each of the four microsites. Sixteen seedlings were planted per replicate site in 4 × 4 plant grids spaced 50-cm apart, giving a total of 512 seedlings. All seedlings were marked with a fire-resistant stainless-steel label. They were watered when transplanted, but no additional treatments were applied. One week after transplanting, the seedlings were checked and those that had died due to transplant shock were exchanged. Seedling survival and the cause of mortality were then recorded 1, 6, 7, 10, 19, and 31 months after transplanting. Causes of mortality were determined visually. Drought-induced mortality was determined when the entire seedling became brown and shriveled with no other physical damage (Plate A). Fire-induced mortality was defined as seedlings that had lost their aboveground parts (only the stainless steel label remaining), plus visual signs of fire damage (Plate B). Seedlings damaged by insects (notably cutworm (Noctuidae)) were distinguished as those showing insect attack, with a smooth cut close to ground level (Plate C). These seedlings mostly had insect filaments. Trampling by ungulates was also classified as a cause of mortality. All causes of mortality not meeting the above criteria were classified as unknown.

Natural establishment of *S. guineense* ssp. *afromontanum* and other forest tree species in miombo woodland

To examine the distribution of naturally occurring establishment of forest tree species within miombo woodland, four 0.25-ha plots, each including all of the four types of microsite, were established. The target species were not only *S. guineense* ssp. *afromontanum*, but other forest tree species as well (Table S1). Observations were conducted in August 2014, before the occurrence of any fires. Crown projection diagrams were created for each individual tree (dbh > 5 cm) in each of the four plots. The relative proportion of tree cover was then calculated by measuring the crown cover of each tree and summing the

area of all tree canopies by species. All seedlings of forest tree species (0.2–1 m in height) were also counted in each plot and their location was recorded (under the tree crown or in the treeless microsite). If a forest tree species was found under a tree crown, the tree crown species was also noted. All individuals were checked for the presence of damage from herbivorous mammals.

Seed deposition of *S. guineense* ssp. *afromontanum*

Seed deposition of *S. guineense* ssp. *afromontanum* was monitored in each of the four replicate microsites from January to March 2012. Seed traps (70 × 70 cm) made of fine-mesh net and with 5-cm-high sides to prevent seeds from being washing away were installed at ground level in each microsite. The total number of seed traps was 96. The seed traps were located 1 m from the main trunk or 1 m from the center of the treeless site. The direction of the first trap was chosen randomly then the remainder were placed at 120° and 240°, respectively. Each seed trap was visited twice a week and the number of *S. guineense* ssp. *afromontanum* seeds was counted.

Data analysis

The statistical analyses were done using R software (ver. 2.14.0; R Development Core Team, <http://www.r-project.org/>). The final percent of seedling survival was analyzed using a general linear mixed model (GLMM). The analyses assumed binomial distribution and used a logit-link function, including fixed effects of microsite type with random effects of individual microsite. The number of seed depositions was also analyzed using a GLMM. The analyses assumed Poisson distribution and used a logit-link function, including fixed effects of microsite type with random effects of individual seed trap. These GLMM were performed using 'lmer4' package³⁰. Significant differences for seedling survival and the number of seed deposition among microsites were conducted using Tukey's post hoc test. The post hoc tests were calculated using the `glht` function in the 'multicomp' package³¹.

Results

Environmental variables

Canopy openness and the percentage of grass cover were significantly lower under *F. natalensis* and *B. floribunda* compared with the treeless sites (Fig. 1). No differences were observed between the *F. natalensis* and *B. floribunda* sites.

Seedling Survival And Causes Of Mortality

Overall, the seedling survival rate of *S. guineense* ssp. *afromontanum* after 2.5 years was 41%; however, rates differed among microsites. Survival was higher under *F. natalensis* and *B. floribunda* than under *U. kirkiana* and in the treeless sites (Fig. 2), but showed no difference between the *F. natalensis* and *B. floribunda* sites. Causes of mortality were determined for 84% of all dead seedlings at the end of the

experiment. Fire was the most important source of mortality (43%), followed by drought (31%), and was higher under *U. kirkiana* and in the treeless sites. Meanwhile, no differences were observed in fire-induced mortality between the *F. natalensis* and *B. floribunda* sites. Insect damage (9%) and trampling by ungulates (1%) resulted in less deaths, and both factors had similar effects in all microsites.

Survival under *U. kirkiana* (Fig. 3-a) and in the treeless microsites (Fig. 3-b) was subsequently compared between those sites in which fire occurred and those in which it did not. The results revealed relatively higher survival in sites where no fire occurred (89% under *U. kirkiana*, 44% in the treeless microsites). No seedlings survived in sites where fires occurred (Fig. 3).

Natural establishment of *S. guineense* ssp. *afromontanum* and other forest tree species in miombo woodland

The ground surface of all four plots was mostly treeless (51.6%), followed by *B. floribunda* (18.7%), *B. boehmii* (11.1%) and *U. kirkiana* (8.4%) (Table 1). *F. natalensis* occupied only 2.9%. Overall, 285 *S. guineense* ssp. *afromontanum* seedlings and 186 (11 species) seedlings of other forest tree species (Table S1) were found in the four plots. Of the 285 *S. guineense* ssp. *afromontanum* seedlings, 146 were found under *F. natalensis*. Similarly, 135 of the additional 186 forest tree species seedlings were also found under *F. natalensis*. Overall, both the *S. guineense* ssp. *afromontanum* and other forest tree seedlings were more closely associated with *F. natalensis* than expected according to crown area. All individuals were checked for damage from herbivorous mammals, with only a few individuals showing damage (15 *S. guineense* ssp. *afromontanum* seedlings and 15 individuals of other forest tree species).

Table 1

Spatial association between microsites and *Syzygium guineense* ssp. *afromontanum* and other forest species seedling in miombo woodland in northern Malawi.

Microsite	Proportion of total cover (%)	Observed number of <i>S. guineense</i> ssp. <i>afromontanum</i> seedling	Expected number of <i>S. guineense</i> ssp. <i>afromontanum</i> seedling	Expected number of other forest species seedling	Expected number of other forest species seedling
Treeless microsite	51.6	3	147.0	1	96.0
<i>Brachystegia floribunda</i>	18.7	25	53.3	9	34.8
<i>Brachystegia boehmii</i>	11.1	34	31.5	17	20.6
<i>Uapaka kirkiana</i>	8.4	41	24.1	1	15.7
<i>Monotes africana</i>	3.2	16	9.2	0	6.0
<i>Ficus natalensis</i>	2.9	146	8.1	135	5.3
Other species	4.1	20	11.7	23	7.6

Seed deposition of *S. guineense* ssp. *afromontanum*

The seed deposition of *S. guineense* ssp. *afromontanum* was varied among four microsites (Fig. 4). No seed was observed under *U. kirkiana* and the deposition data from these sites were excluded from the subsequent analysis. Most (85%) of the seeds were deposited under *F. natalensis*, with significantly more seeds deposited under *F. natalensis* than other microsites.

Discussion

Protection from fire appears to be the most important facilitation mechanism affecting increased survival of forest tree species in miombo woodland in northern Malawi. Overall, fire was the cause of 43% of *S. guineense* ssp. *afromontanum* seedling deaths, suggesting that fire is the principal driver of seedling mortality (Fig. 2). The majority (89%) of mortalities occurred in the treeless sites and under *U. kirkiana*, where grass cover was high, thereby increasing the fuel load. In contrast, fire-induced mortality was very low under *F. natalensis* and under *B. floribunda* (4 and 23%, respectively). In both sites, fire is thought to be inhibited due to the closed crown, which prevents light-demanding C4 grasses from establishing³². This effect, combined with the changes in microclimatic conditions provided by the closed crown, drastically decrease overall flammability. Since the intervals of the seedling monitoring was long, I may overestimate the effect of fire on the seedling mortality. I cannot rule out the possibility that seedlings were dead because of factors other than fire, but, fire burned the dead individual after the seedling death.

However, the seedling survival in treeless microsite and under *U. kirkiana* in which fire did not occur was relatively high (Fig. 3). These results suggest that *S. guineense* ssp. *afromontanum* seedlings can survive in miombo woodland in the absence of fire.

Drought was the second most important factor of the seedling mortality (31% in total death), but less individual under *F. natalensis* and *B. floribunda* were dead due to drought compared with treeless microsites (Fig. 2). It was previously suggested that protection from drought plays a key facilitative role in many stressful ecosystems^{33,34,35}. Further long-term studies are now required to determine the relative importance of fire and drought on the mortality of forest tree species during the forest expansion.

In this study, no seedlings died due to damage by vertebrate herbivore during the 2.5-year study period, suggesting that vertebrate herbivore is not an important factor in seedling mortality in miombo woodland. Rao et al., (2003) suggested that although vertebrate herbivore has a limited impact on seedlings at an early stage, it becomes more critical at later stages when seedlings grow taller and become more visible to ungulates³⁶. However, the observations of natural establishment in this study revealed only a few individuals with grazing damage, suggesting that vertebrate herbivores have a limited impact on the establishment of forest tree species in this region, even at later stages. This was surprising given that herbivorous mammals, along with fire, pose a major constraint on tree establishment in African savannah-woodland^{37,38}. Although the reason for my finding is unknown, it may be attributed to the decrease in herbivores resulting from human impacts such as hunting.

Soil fertility is generally higher in tropical forest than in adjacent savannah-woodland^{39,40}, and some studies suggest that the nutrient-poor soil of savannah-woodlands limits the establishment of forest tree species, preventing forest development. Thus, it is possible that the successful seedling survival observed under *F. natalensis* and *B. floribunda* was the facilitative effect of increased soil nutrient availability. Increased soil nutrients under nurse plants is a widely known mechanism of facilitation⁴¹; however, recent studies suggest that soil nutrient availability itself has little effect on seedling survival of forest tree species⁴⁰. For example, Viani et al., (2011) compared seedling survival of three forest tree species between nutrient-rich forest soil and nutrient-poor savannah soil, and found no differences in survival that could be linked to the soil origin⁴⁰. Thus, it was hypothesized that soil nutrient availability had a limited effect on seedling survival of *S. guineense* ssp. *afromontanum*, even under increased soil nutrient availability in the *F. natalensis* and *B. floribunda* sites. Future studies are now needed to examine this further and fully understand the facilitative effects on the establishment of forest tree species.

The findings also suggest that *B. floribunda* offers a similar degree of protection from fire as *F. natalensis*. In fact, seedling mortality due to fire and seedling survival did not differ between the *B. floribunda* and *F. natalensis* sites (Fig. 2). However, natural establishment of *S. guineense* ssp. *afromontanum* and other forest tree species tended to be concentrated under *F. natalensis*, with few seedlings under *B. floribunda* (Table 1). These results suggest that the facilitative mechanism of fire suppression does not fully explain the recruitment of forest tree species in the miombo woodland, indicating the involvement of other processes. I suggest that the pattern of seed deposition by

frugivorous animals is critical for the recruitment of forest tree species. In this study, higher seed deposition of *S. guineense* ssp. *afromontanum* was observed under *F. natalensis* than in the other three microsites. Moreover, the forest tree species observed under *F. natalensis* were largely animal dispersed, further supporting the hypothesis.

In conclusion, this study highlights the potential mechanisms of forest tree species establishment in miombo woodland. The findings suggest that the closed crown of *F. natalensis* is less likely to be burnt, increasing survival of *S. guineense* ssp. *afromontanum* seedlings on the ground below. Fire suppression is very important because forest tree species are generally very vulnerable to fire^{8,10,11}. Previous empirical and theoretical studies on forest-savannah dynamics further suggest the importance of fire suppression on forest expansion into adjacent savannah-woodland^{3,42}. However, present study also suggests that fire suppression is not the only factor affecting the establishment of forest tree species. Fire is also unlikely to occur under the closed crown of *B. floribunda* (Fig. 2) but few forest tree species were naturally established in these sites (Table 1). Overall, these findings suggest that in addition to fire suppression, dispersal limitations also play a role in forest-savannah dynamics in this region, especially at the community level.

Declarations

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Author Contributions

TF conceived, designed, and executed this study and wrote the manuscript. No other person is entitled to authorship.

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Figures

Figure 1

Boxplot of canopy openness (a) and proportion of grass cover (b) measured in northern Malawi. All microsites were located in miombo woodlands. Different letters indicate significant differences ($P < 0.05$) among the microsites based on Steel Dwass's post hoc tests

Fig. 2

Figure 2

Fate of Syzygium guineense ssp. afromontanum transplants in four microsites after 2.5 years. Seedling survival ($n = 512$) was measured from February 2012 to August 2014. All microsites were located in miombo woodlands. Different letters within each fate class indicate significant differences ($P < 0.05$) based on Tukey's post hoc tests.

Fig. 3

Figure 3

Comparisons of seedling survival between those sites in which fire occurred and those in which it did not.

Fig. 4

Figure 4

Mean number of dispersed seeds of *Syzygium guineense* ssp. *afromontanum* (± 1 SE) at four microsites in northern Malawi. All microsites were located in miombo woodlands. Seed rain was monitored from January to March 2012. Different letters within each fate class indicate significant differences ($P < 0.05$) based on Tukey's post hoc tests.

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