

Full Length Research Paper

# The woodland tree *Brachystegia floribunda* facilitates the encroachment of forest tree species into miombo woodlands in northern Malawi

Tomohiro Fujita

Graduate School of Asian and African Area Studies, Kyoto University, Japan.

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Although, human activities have caused major losses of tropical forest, there are also reports of forest encroachment and expansion into surrounding sparse vegetation types (savannah and woodland). Large savannah-woodland trees may promote forest encroachment into their surroundings by facilitating seed deposition and subsequent establishment of forest species. This work sought to determine whether large individuals of the woodland tree *Brachystegia floribunda* facilitate encroachment of montane forest tree species. To this end, environmental parameters, seed rain and seedling distribution of montane forest tree species were examined in south-east Africa. The seed rain and the numbers of tree seedlings were both higher below large *B. floribunda* trees than below: (i) small specimens of this woodland tree and (ii) in open grassland. Moreover, large individuals of *B. floribunda* modified microhabitat conditions more than small trees. Thus, large *B. floribunda* trees probably facilitate the encroachment of montane forest trees into surrounding woodlands.

**Key words:** *Brachystegia floribunda*, tropical forest, grassland, woodlands.

## INTRODUCTION

Savannah and/or woodland habitats interspersed with closed-canopy forest are common in many tropical regions (Hennenberg et al., 2006). Although, there has been a major loss of forest area in these regions due to factors such as logging (Nepstad et al., 1999); studies have also documented the encroachment and expansion of forest into more open vegetation types (Banfai and Bowman, 2007; Mitchard et al., 2009; Bowman et al., 2010). Generally, forest trees seldom establish adjacent to these sparsely vegetated areas, because the open vegetation is often more resistant to fire and water stress and competition from grass species (Shararm et al., 2009); however, these limiting factors may not apply under a savannah-woodland tree (Hoffmann, 2000). By providing shade, savannah-woodland trees can suppress the growth of grass, leading to less frequent occurrence

of fires and less competitive conditions (Shararm et al., 2009). A tree can also improve water status by reducing solar radiation (Shararm et al., 2009). In addition, seed dispersal can be greater below trees than in a treeless grassland, because bats and birds may be more likely to visit tree crowns than grassland. Thus, savannah-woodland trees adjacent to forest may play an important role in forest encroachment (Rolhauser et al., 2011).

The effect of savannah-woodland trees on promoting forest tree encroachment may vary depending on tree size. Seed rain may be greater below large trees than small trees, because bats and birds are more likely to perch on taller, large-crowned trees than on the smaller crowns of short trees (Aukema and Martínez del Río, 2002; Lasky and Keitt, 2012). Seed deposition below large trees may be important in establishing forest tree

seedlings, as their crowns may create a better environment for seedling germination and survival than the smaller crowns of short trees. The present study examined the role played by woodland trees in the encroachment of forest trees in northern Malawi (south-eastern Africa). In south-central Africa, about 2.7 million km<sup>2</sup> are covered with miombo woodland made up of leguminous species in three closely related genera: *Brachystegia*, *Julbernardia*, and *Isoberlinia* [Fabaceae subfamily Caesalpinioideae (Campbell et al., 1996)]. These areas also contain patches of lowland rain, montane rain, and riparian forests, all of which differ from miombo woodland in floristic composition and structure (White et al., 2001). The vegetation dynamics between these forests and miombo woodlands are unclear (White, 1983). Experiments have shown that the forests expand into miombo woodland when fires are prevented (Trapnell, 1959; White et al., 2001); miombo woodland, especially in wetter regions, can be an alternative stable state to forest.

The present study focused on the role of *Brachystegia floribunda* as a facilitator of montane forest tree encroachment. This species was chosen because large numbers of forest tree saplings occur under the dense canopy of *B. floribunda* (Fujita submitted), which is generally the dominant tree in miombo woodland (White, 1983) and in the study area. The dry pods of the species are explosively dispersed (Chidumayo and Frost, 1996), and the seed itself does not attract frugivores. However, non-fruiting trees may attract as much outside seed rain as do fruiting trees by providing a calling perch and shelter from predators (Carriere et al., 2002). In this context, the following specific postulates were tested. First, tall *B. floribunda* individuals modify microhabitat conditions differently from short trees or grasses in treeless vegetation openings. Second, the seed rain of forest trees is greater below tall *B. floribunda* trees than below short trees or grasses in treeless opening. Third, the number of forest tree seedlings is highest below tall *B. floribunda* trees, reflecting greater seed input and beneficial environmental modifications.

## MATERIALS AND METHODS

### Study area

The study was conducted in the periods of January to March 2012 and August to September 2012 on private land located in a rural zone managed by the villagers of Ntchuka (10° 58' S, 34° 04' E) on the north Vipya Plateau in northern Malawi. The region is vegetated predominantly by miombo woodland, although, there are stands of montane rain forest on mountain crests (above ~1800 m elevation), in valleys, and on mountainous slopes (1700 to 1800 m elevation). The size of these patches varies from about 10 m<sup>2</sup> to ~1 ha. The mean annual rainfall on the north Vipya Plateau exceeds 1270 mm, which is distributed across a wet season from December to April, with a dry season from May to November (Chapman, 1970). The Vipya Plateau is underlain by undifferentiated basement complex rocks that are mainly gneisses (Chapman, 1970). The soil of the study area was a well-drained red and sandy clay loam. Most of the

private land area other than montane forest and other forest patches is burnt by the local inhabitants at intervals of 2 to 3 years during the late dry season (September to December). Fires are set to clear footpaths, as paths overgrown by tall grass become difficult to traverse and dangerous due to the presence of snakes.

Montane forests are typically less flammable due to the dense canopy that excludes grasses and maintains a more humid understory. Therefore, fire is unlikely to penetrate far into the forest. Few trees are harvested from this area of private land, as it is located far from local villages.

### Measurement of standing trees

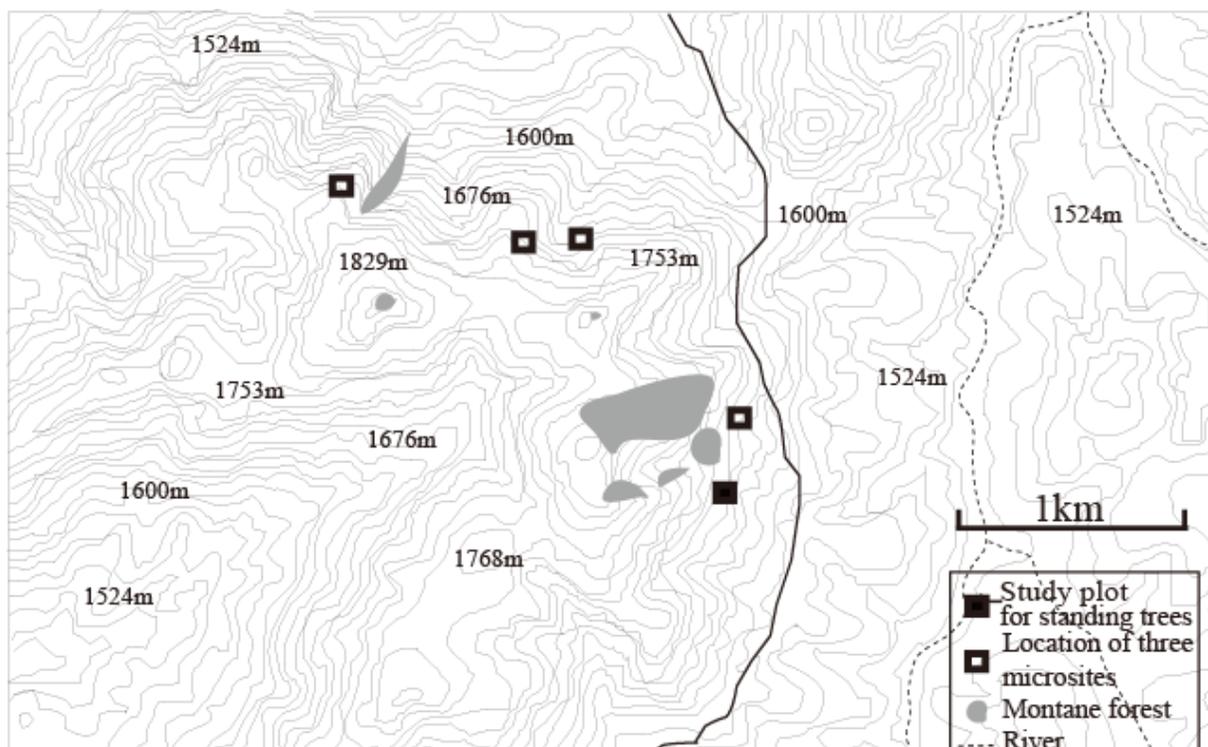
To describe the vegetation structure in the study area, all standing trees were measured in a 50 × 50 m plot established on a mountainous slope bearing miombo woodland. The plot was located about 100 m from a montane forest. In the plot, all mature trees of more than 1 cm in Diameter at Breast Height (DBH) were identified, and their height and crown radius were measured. The DBH of trees greater than 5 cm was also measured.

### Experimental design

Environmental parameters, seed rain and seedling densities of montane forest trees were measured in three microhabitats: a treeless opening (hereafter, open microsite), a site beneath short *B. floribunda* trees (<3 m tall; hereafter, short-tree microsite) and a site beneath tall *B. floribunda* trees (>5 m tall; hereafter, tall-tree microsite). The open microsite lacked both mature trees and a canopy cover. The microsites were generally round in shape with radius of 2 m. The sizes of tree microsites (short-tree or tall-tree) exactly matched the crown areas above them. Three microsites of each type were located in miombo woodland located at least ~50 m from the montane forest (Figure 1). Short-tree and tall-tree microsites were established within 20 m of one another. Open microsites were located at least 10 m from short-tree and tall-tree microsites. Five replicates of each microsite type were established.

### Measurement of environmental conditions

Environmental parameters were measured in each replicate of the three microsite types (n = 15). Parameters selected included above-ground microclimate variables, soil water content, and the proportion of grass cover. To estimate canopy openness, four hemispherical canopy images were taken at each microsite 1-m above ground using a fish-eye wide-angle lens (Raynox DCR-CF; Yoshida Industry Co., Ltd., Tokyo, Japan). The images were captured at the midpoint of the crown radius in each of the cardinal directions from trunks of short and tall trees. At the open microsite, the photographs were taken at 1-m in each of the cardinal directions from its centre. The hemispherical photographs were taken during the rainy season (February 2012). Gap light analyser software (Frazer et al., 1999) was used to calculate canopy openness. The overall canopy openness at each microsite was calculated as the mean of the four values. Air temperature and relative humidity (RH) were measured with a data logger (T and D, Ondotori RH TR72U, Matsumoto, Japan) 1 m from the trunks of short and tall trees and at the centre of the open microsite. The measurements were made on 1 to 2 September 2012. Soil water content at 12-cm depth was measured using time domain reflectometry (TDR) probes (Campbell Scientific, Hydrosense, Townsville, Australia) during the rainy season of March 2012 and the dry season of September 2012. The soil water content measurements were taken at the same points at which the canopy openness photographs were taken.



**Figure 1.** Map of the study plots, microsites and montane forest patch. One of the replicates of microsites (open, short-tree, tall-tree) exists within study plot for standing trees. Thus, only four replicates of microsites are shown in the map. Miombo woodland surrounds the montane forest patch.

The overall soil water content at each microsite was calculated as the mean of the four values. To estimate the proportions of grass cover, three quadrats (each 1 × 1 m) were established at 1 m from each tree bole (short-tree and tall-tree microsites) and at the centres of open microsites. The direction of the first quadrat was determined haphazardly, and the other quadrats were placed on bearings 120 and 240° from the direction of the first quadrat. In each quadrat, the proportion of grass cover was visually estimated using 10% cover-class intervals. The overall proportion of grass cover at each microsite was calculated as the mean of the three values.

#### Measurement of seed rain and seedling density

Seed rain was measured between January 2012 and March 2012 (rainy season). During the rainy season, many montane forest tree species bear fruit (Dowsett-Lemaire, 1985). Seed traps were installed where the quadrats had been located. The traps each comprised a 70 × 70 cm sheet of fine-mesh net secured to the ground (14,700 cm<sup>2</sup>/microsite). Each net had sides 5 cm high that prevented seed from washing away, but allowed for entry of seed predators. Thus, the seed rain values may be underestimated. Initially, a conventional method was used to measure seed rain (traps were inverted cones of polyethylene cloth with circular mouths of polyethylene pipe; each was supported by three vertical PVC plastic pipes adjusted so that the receiving face was 1 m above the ground). However, these traps were easily visible and were damaged by local villagers. Each microsite was visited and collected from twice a week; seeds were identified and counted. The seed rains in replicate traps at each microsite were combined for analysis. Only the number of montane forest tree seeds is reported here, as the focus of this study was on encroachment of

forest trees into miombo woodland. Montane forest trees were defined following Friis (1992) and White et al. (2001), as tree species that occur mainly in montane rain forests.

Before setting the seed traps, all montane forest tree seedlings (30 cm ≤ H ≤ 130 cm) were counted in quadrats in which the proportions of grass cover had been estimated. The seedlings were identified by an expert from the national herbarium and botanical gardens of Malawi.

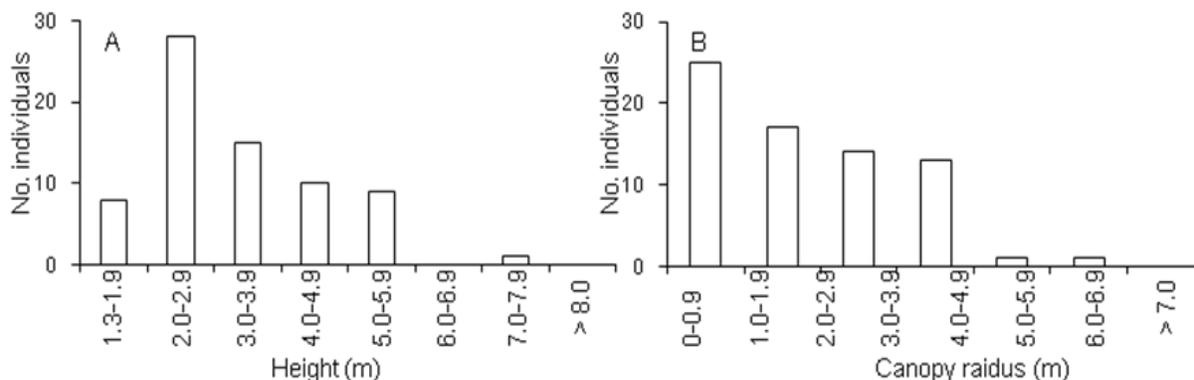
#### Data analysis

Data were checked for normality using the Kolmogorov-Smirnov test and for homoscedasticity using the Bartlett test. The data for the proportion of grass cover, density of seed rain, and seedlings of montane forest tree were analysed using nonparametric methods, as the data violated the assumption of homoscedasticity. Differences in these values among microsites were compared using the nonparametric Steel-Dwass multiple comparisons test. Tukey-Kramer multiple comparison tests were used to detect differences in canopy openness, soil water content, mean air temperature and RH among microsites. All statistical analyses were conducted with R software ver. 2.12.2 (R Development Core Team, 2011).

## RESULTS

### Composition and structure of standing trees

In total, 198 individuals from 13 species of standing tree (DBH > 1 cm) were recorded. The basal area (BA) was



**Figure 2.** Height (A) and canopy radius (B) distribution of *Brachystegia floribunda* in study plot (0.25 ha).

**Table 1.** Environmental conditions (n = 5 per microsite) measured among three microsites (means  $\pm$  SE).

Variable	Open	Short-tree	Tall-tree
Canopy openness (%)	71.1 $\pm$ 9.3a	29.9 $\pm$ 6.9b	18.9 $\pm$ 4.7b
Ta ( $^{\circ}$ C)	25.2 $\pm$ 0.8a	21.9 $\pm$ 0.4b	21.4 $\pm$ 0.4b
RH (%)	42.1 $\pm$ 2.5a	49.9 $\pm$ 1.8b	51.9 $\pm$ 1.3b
SWC (rainy season) (%)	27.6 $\pm$ 1.2	31.3 $\pm$ 1.4	30.4 $\pm$ 1.6
SWC (dry season) (%)	5.3 $\pm$ 0.8	4.8 $\pm$ 0.2	4.9 $\pm$ 0.3
Grass cover (%)	58.0 $\pm$ 4.5	48.0 $\pm$ 6.5	22.7 $\pm$ 9.0

See text for microsite definitions. Variables: Ta, mean air temperature; RH, relative humidity; SWC, soil water content. Variables for which significant differences between microsite were found are in bold. Different letters show significant differences at  $\alpha < 0.05$  for the same variable.

6.6 m<sup>2</sup>/ha, tree density was 0.08 individuals/m<sup>2</sup> and the median DBH was 8.4 cm. *B. floribunda* made up the vast majority (> 90%) of the basal area. The analyses presented here were conducted exclusively on *B. floribunda*. The height distribution and crown radius of *B. floribunda* had a right-skewed distribution (skewness = 3.02,  $P < 0.01$ , height; skewness = 2.16,  $P < 0.05$ , crown radius). Although, most trees were fairly short (half were < 3 m) and small-crowned (half were < 2 m), a few were tall and large-crowned (Figure 2).

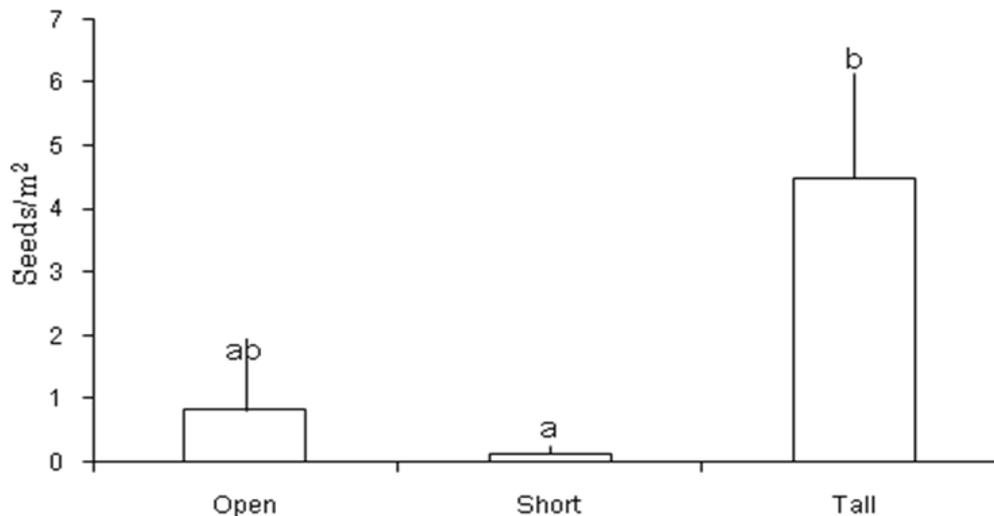
### Microhabitat characterisation

Table 1 shows the environmental variables. Canopy openness and mean air temperature were significantly lower in the short- and tall-tree microsites than in the open microsite, but similar between the short- and tall-tree microsites (Tukey-Kramer test;  $p = 0.55$ , canopy openness;  $p = 0.85$ , mean air temperature). RH was higher in the short- and tall-tree microsites than in the open microsite, but similar between the short- and tall-tree microsites (Tukey-Kramer test;  $p = 0.75$ ). Soil water content did not differ among microhabitats in either the rainy (one-way ANOVA;  $p = 0.17$ ) or dry seasons (one-way ANOVA;  $p = 0.79$ ). The proportion of grass cover in the tall-tree microsite tended to be lower than that in the

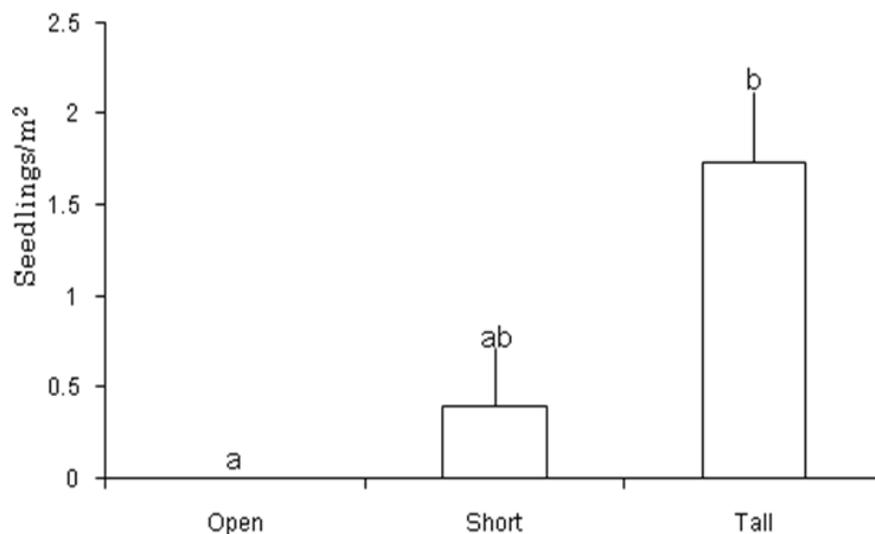
open and short-tree microsites, although, there were no differences between these latter sites (Steel-Dwass test;  $p = 0.09$ ) or between the short- and tall-tree microsites (Steel-Dwass test;  $p = 0.14$ ).

### Seed and seedling density of montane forest trees

In all, 40 seeds of montane forest trees from three species were found: *Parinari excelsa* Sabine (Chrysobalanaceae), *Apodytes dimidiata* E. Mey. (Icacinaceae) and *Syzygium guineense* ssp. *afromontanum* (Willd.) DC. (Myrtaceae). The seeds of these species are dispersed by animals. The seeds were found in all three microsites, but most (83%) were found in the tall-tree microsite (Figure 3). The seed density was significantly higher in the tall-tree microsite than in the short-tree microsite (Steel-Dwass test;  $p < 0.05$ ). Furthermore, there was a tendency towards higher seed densities in the tall-tree microsite (in comparison to open microsites), but this between-site difference was not significant (Steel-Dwass test;  $p = 0.10$ ). Thirty-two seedlings of montane forest tree from five species were found: *Cussonia spicata* Thunb. (Araliaceae), *Diospyros whyteana* (Hiern) F. (Ebenaceae), *A. dimidiata*, *Rapanea melanophloeos* (L.) Mez (Myrsinaceae) and *S. guineense* ssp. *afromontanum*. The seeds of all of these trees are also



**Figure 3.** Mean seed density of montane forest in the three microsites. Error bars = 1 SE. Different letters indicate statistically significant differences between microsites at the  $P < 0.05$  level.



**Figure 4.** Mean seedling (30 cm  $\leq$  H  $\leq$  130 cm) density of montane forest in the three microsites. Error bars = 1 SE. Different letters indicate statistically significant differences between microsites at the  $P < 0.05$  level.

dispersed by animals. The seedlings were found in short- and tall-tree microsites, but not in the open microsite. There was a tendency towards higher seedling density in the tall-tree microsite (in comparison to the short-tree microsite) (Figure 4), but this between-site difference was not significant (Steel-Dwass test;  $P = 0.09$ ).

## DISCUSSION

### Seeds of montane forest trees in miombo woodland

The deposition of seeds of montane forest trees was confirmed in all three microsites, but most were found in

the tall-tree site (Figure 3). The greater seed rain at this site was probably related to the number of birds that preferentially perch on tall and large-crowned trees (Aukema and Martínez del Río, 2002; Lasky and Keitt, 2012). Bird preferences are most probably related to better calling sites in large trees, or better protection from predators (McDonnell, 1986; Roxburgh and Nicolson, 2008). This outcome is consistent with previous research showing that there are large seed rains beneath tall tree individuals located in abandoned fields (McDonnell, 1986; Slocum and Horvitz, 2000). McDonnell (1986) suggested that perch height relative to neighbouring perches, not absolute height, has the most influence on attracting birds.

This may be the case in this study as well. Tall trees (5 m < height) were the tallest structures in the vicinity and were relatively scarce in the study area (Figure 2A). The results indicate that tall *B. floribunda* trees may act as dispersal foci (Clark et al., 2004) for montane forest trees as they encroach into miombo woodland.

The present results suggest that tree height may partly influence the seed deposition of montane forest trees into miombo woodland. However, other factors such as canopy architecture (Slocum and Horvitz, 2000), forage density (Howe, 1979) and mistletoe infection (their fruits attract frugivores) may also influence seed-deposition patterns of montane forest trees. Future studies should include these factors and examine the spatial pattern of seed deposition.

### Seedling establishment of montane forest trees in miombo woodland

Seed arrival is the first step in forest tree encroachment into other vegetation types. The establishment of forest trees after seed arrival is limited by many factors such as repeated fires (Hoffmann, 2000), competition with grasses (Holl, 2002), water stress (Bowman and Panton, 1993), low soil fertility (Kellman and Miyanishi, 1982), seed predation by rodents (Holl, 2002) and browsing by antelope (Sharam et al., 2009). In this miombo woodland, the establishment success of montane forest trees seems to be facilitated by the presence of *B. floribunda* (Figure 4). Potential mechanisms that may allow montane forest trees to establish in miombo woodlands are presented as follows:

Amelioration of water stress can be important in establishing montane forest trees in miombo woodland (Holl, 1999). Lower canopy openness and air temperature and higher RH in tall-tree microsites, compared to the open microsite (Table 1) can reduce leaf temperature and transpiration loss, consequently, inducing a more favourable water balance in tree seedlings. These modifications could be critical for seedlings to withstand drought, even without improving soil water conditions, as found by Gomez-Aparicio et al. (2005). Reduced grass cover in the tall-tree microsite (Table 1) may also have a positive effect on the establishment of montane forest trees. For example, less grass cover may decrease the occurrence of fire.

Hennenberg et al. (2006) showed that fires occur frequently with high grass cover, but rarely with low grass cover. Suppressed fire occurrence is crucial for the survival of montane forest trees, which have a low resistance to fire (Lawton, 1978; Kikula, 1986). In Africa, including this region, fire-exclusion experiments have resulted in closed forest stands (Swaine et al., 1992; White et al., 2001). Low grass cover may also reduce competition for seedlings. Several studies in tropical regions have shown that competition with grasses reduces seedling survival and growth (Holl, 2002; Sharam et al., 2009). The present

study suggests that tall *B. floribunda* trees facilitate not only seed arrival, but also the establishment of montane forest trees in miombo woodland.

Unexpectedly, aboveground microclimatic factors and soil water content did not differ significantly between the tall- and short-tree microsites (Table 1). However, the proportion of grass cover tended to be higher in the short-tree microsite (Table 1). The difference in the proportion of grass cover can critically influence the establishment of montane forest trees, as high grass cover induces some negative effects, as described earlier.

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