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Seed and seedling survival of African mahogany (*Entandrophragma* spp.) in the Central African Republic: Implications for forest management

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Abstract

African mahoganies of the genus *Entandrophragma* are among the most valuable and important timber species harvested in Central Africa, representing more than 70% of total export volume from many areas. In spite of the importance of these species, relatively little is known about their regeneration ecology and little effort has gone into understanding the reasons for the consistently reported regeneration failures after logging. I assessed seed survival to germination (*Entandrophragma angolense*) and seedling survivorship (*E. cylindricum*) in three different forest types – monodominant *Gilbertiodendron*, mixed species, and fallow forest – under three different treatments – control, small mesh chicken wire, and large mesh chicken wire – to evaluate the relative importance of different causes of mortality. All seeds were eaten in controls and in both exclosure treatments within *Gilbertiodendron* forest in a matter of days. Seed survivorship to germination within exclosures in mixed species and fallow forest increased by approximately 10 and 25%, respectively, compared to *Gilbertiodendron* forest. Six-month seedling survivorship in controls was 37, 12, and 9% in *Gilbertiodendron*, mixed species and fallow forest, respectively. Seedling mortality was due to different causes in each forest type. In *Gilbertiodendron* forest controls, an equivalent percentage of seedlings died due to fungal and insect attack (27 and 28%, respectively), while in mixed species forest controls 28 and 55% of seedlings died of these causes, respectively. In fallow forest controls, 48% of seedlings died from predation and/or uprooting by small mammals, all in the first few weeks post-sowing; insect attack (26%) and drought (13%) were other important causes of seedling deaths. Protecting seedlings with exclosures had a dramatic effect on seedling survivorship within the fallow forest, increasing to over 50%.

Because of their exceptional value, out or enrichment planting of these species may be economically viable both as part of forest management and agroforestry systems. Thus, planting out seedlings of these species in mixed species and fallow forest gaps with the appropriate soil chemical composition after the period of potential dry season and small mammal vulnerability is recommended.

Keywords: Agroforestry; Central Africa; Granivores; Predation; Seedling mortality; Tropical forest management

1. Introduction

Even though international trade in African tropical timber dates back well over a century, its importance in terms of impact on Central Africa's national economies and timber production has increased significantly in recent decades (Anonymous, 2005). The installation of sawmills has transformed isolated villages into logging towns, abruptly linking them to the global economy (Robinson et al., 1999). The subsequent cascade of effects on the local environment – increased immigration, increased land conversion for agriculture, increased reliance on the forest for construction materials and non-timber forest products, and the commercialization of hunting – has been well documented and much discussed (Wilkie et al., 1992; Makana and Thomas, 2006; Zhang et al., 2006).

With the notable exception of Gabon, the recent wave of timber exploitation within Central Africa has been dominated by the extraction of African mahoganies, most notably of the genus *Entandrophragma* (Plouvier, 1998; Hall et al., 2003b; ITTO, 2004). Even though densities of exploitable African mahoganies typically range between 1 and 2 individuals ha^{-1} in unlogged, mahogany "rich" forests (for all species combined; CTFT, 1985; Letouzey, 1985; Hall et al., 2003b), the price these species

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command on international timber markets justifies the expense and effort of undertaking logging operations within the most remote forests of Central Africa. As with the true mahogany, *Swietenia macrophylla*, the highly selective "high grade" logging practiced throughout Central Africa often leads to regeneration and/or recruitment failure where natural regeneration is insufficient to replace harvested stems on a time scale required for sustainable timber production (Hall et al., 2003b; Grogan and Galvão, 2006). Because poorly conceived logging operations in the tropics are often the precursors to degradation and forest conversion (Plouvier, 1998; Curran et al., 2004; Makana and Thomas, 2006), it is essential that management interventions be designed to foster long-term sustainability.

Important research designed to inform forest management has been undertaken in recent years to understand the ecology of African mahoganies. The species typically logged in Central Africa – *Entandrophragma angolense*, *E. candollei*, *E. cylindricum*, and *E. utile* – are canopy emergents classified as non-pioneer light demanders, or species that establish as seedlings in deep shade but need to be released in order to develop (Hawthorne, 1995; Hall et al., 2003c). Seedlings of these species have been shown experimentally to develop best in approximately 25% full sunlight (Synnott, 1975; Pieters, 1976; Swaine et al., 1997; Agyeman et al., 1999; Hall et al., 2003c). Hall et al. (2004) linked adult meso-scale spatial distribution patterns of three of these four *Entandrophragma* spp. (*E. angolense*, *E. candollei*, and *E. cylindricum*) to edaphic factors and suggested that growth performance helps explain adult tree distribution of *E. candollei* and *E. cylindricum* seedlings in relation to soil fertility (Hall et al., 2003a).

In spite of the fact that considerable research has been undertaken to improve natural forest management of *Entandrophragma* spp., important gaps remain in understanding early seed and seedling establishment phases. For example, Medjibe and Hall (2002) and Petrucci and Tandeau de Marsac (1994) documented abundant wind-aided seed dispersal of *Entandrophragma* spp., while Hall et al. (2003b) reported seedling densities of one individual m^{-2} across a 100 ha fixed plot in mixed species forest. However, Hall et al. (2003b) noted that seedling carpets in mixed species forest typically disappear within a year. Because *Entandrophragma* spp. can persist in deep shade and on poor soils, it is clear that several factors, including seed predation (Synnott, 1975), contribute to seed and seedling mortality. Given that both mortality rates and factors may vary with forest type, it is important to understand differences in order to manage these species within specific forest types to favor their early development.

This study was undertaken to describe seed and seedling mortality patterns of the African mahoganies *E. angolense* and *E. cylindricum* in different forest types in order to provide improved management guidelines for timber production. Specific questions asked were: (1) is seed and seedling survivorship the same among monodominant *Gilbertiodendron*, mixed species, and fallow forests? (2) Are factors leading to mortality the same between these forest types? (3) How might this information be applied to both natural forest management and agroforestry systems?

2. Materials and methods

2.1. Study site

This research was undertaken in the Dzanga-Sangha Dense Forest Reserve in southwestern Central African Republic (2°14′ to 3°25′N; 15°40′ to 16°32′E). The climate is characterized by a long wet season during which the most pronounced rains fall between late August and mid November; a pronounced dry season extends from the end of November through early March. Annual precipitation was 1365 mm from 1973 to 1985 (Carroll, 1997); mean temperature varies between 24 °C (December) and 29 °C (April). Soils within the study area are generally classed as oxisols but with important variability in fertility within the study site (see Hall et al. (2004) for further description).

Harris (2002) distinguished seven forest types within the Reserve, excluding areas recently converted to and/or recovering from agriculture. Mixed species forest covers over 50% of the Reserve's *terra firma* area (Hall, 2002), while *Gilbertiodendron* forest is also a major Reserve component. Unlogged mixed species forest is characterized by a semi-broken canopy where treefall gaps generally contain one to several uprooted trees. This forest typically has between 100 and 120 species of woody plants $\geq$10 cm diameter ha^{-1} with a stem density of approximately 450 individuals ha^{-1} and a basal area of 30.5 m^2 ha^{-1} (Hall et al., 2003b). In contrast, *Gilbertiodendron* forest is characterized by a closed canopy where treefalls are most often single stems broken off near the base or from the bole of the tree. The stem density and basal area of this forest type is dominated by *Gilbertiodendron dewevrei*, which typically represents 57% of stem density and 74% of basal area. Species richness for trees >10 cm diameter is much lower in *Gilbertiodendron* forest than in mixed species forest, with only 49 species ha^{-1}; stem density and basal area were found by Hall and Harris (unpublished data) to be 291.5 individuals ha^{-1} and 29.8 m^2 ha^{-1}, respectively. For the purposes of this study, fallow forest refers to agricultural fields that have been left fallow between 2 and 7 years and where the pre-agricultural vegetation was mixed species forest.

2.2. Experimental design

Three different forest types (*Gilbertiodendron*, mixed species, and fallow forest) were chosen to assess mortality factors for *Entandrophragma* spp. seeds and during the early seedling stage. Four replicate sites were chosen within each forest type and three different treatments (no wire mesh control, 0.5 cm × 0.5 cm wire mesh, and 2.0 cm × 2.0 cm wire mesh) were applied over a 1 × 2 m area, with different mesh sizes assumed to exclude different-sized seed and seedling predators. At each site wire mesh was buried in the soil to approximately 5 cm depth and closed on top to form a cage capable of excluding rodents and other small mammals. All treatments within a site were within 100 m of each other. Within each replicate treatment 30 seeds of *E. angolense* were randomly scattered across the forest floor and 30 recently germinated (∼1 week) *E. cylindricum* were bare-root transplanted into the soil. Thus, a total of 1080 seeds (30 × 3 treatments × 4 replicate sites × 3 forest types) and 1080 seedlings were used to begin this experiment. Seedlings were planted in addition to seeds to assure sufficient seedling sample size for analysis because Synnott (1975) found granivore predation to be an important source of seed mortality for *E. utile* at his study site in Budongo Forest, Uganda.

Seed presence and condition – germinated or not – were noted during each observation. Four classes of mortality (small mammal, fungal attack, insect attack, and drought) were noted with respect to seedlings. Observations were recorded weekly for a period of 42 days for seeds at which point all seeds had either suffered mortality or germinated, and for 190 days for seedlings. The experiment began during a peak period of *E. cylindricum* fruiting and seed dispersal during the wet season (end September 2000) and continued through the subsequent dry season (end November 2000 – early March 2001), ending in April 2001 after the return of the rains. Small mammal attack was scored when teeth marks were left on seeds or cotyledons and/or when clear evidence of uprooting of seedlings was present. Small mammal attack was also scored when seeds were removed (Synnott, 1975). Seedlings were scored as succumbing to fungal attack when leaves wilted and were covered with fungi or became discolored and/or covered with a moist film. Insect attack was recorded when cotyledons, leaves and/or leaflets appeared consumed by insects. Drought was recorded as the source of death when seedlings were noted on successive observation dates as wilted and clearly dried up.

2.3. Data analysis

Logistical constraints were such that it was impossible to consistently collect data at two remote *Gilbertiodendron* stands; however, data were recorded intermittently and at the end of the experiment. For this reason, data from these sites were unavailable for analysis when comparing sources of seedling mortality. Two additional data sets were excluded from analysis – one from mixed species and one from fallow forest – due to theft of wire mesh cages and problems with data collection. Thus, for analysis of sources of seedling mortality within *Gilbertiodendron* forest, data from only two sites were used. For the other two forest types, data from three sites were used for analysis. Data from all sites were used for seed exclosure experiments as all sites were consistently followed through germination or seed mortality. Data were averaged by treatment within site.

Seed and seedling data were analyzed using randomization tests in EcoSim (Gotelli and Entsminger, 2001). A χ^2 statistic was calculated from contingency tables and then compared to the distribution of 1000 χ^2 statistics calculated from randomly generated contingency tables based on the original data. When the actual χ^2 statistic fell outside the 95% confidence interval (i.e., <25th or >975th value) the null hypothesis was rejected and it was concluded that significant differences in mortality or sources of mortality existed.

The χ^2 analyses were conducted to determine whether seed survival to germination was different among forest type controls as well as to determine whether or not survival was different among treatments within forest types. Seedling survivorship and sources of mortality were compared among forest treatment controls as well as among treatments within each forest type.

3. Results

3.1. Seed survival to germination

Seed predation by granivores was so intense in *Gilbertiodendron* forest that small mammals managed to dig under or squeeze through holes in the cages and eat all seeds in all treatments. Even when holes were repaired, mesh reburied, and seeds replaced within exclosures, small mammals still managed to break in and consume all seeds. While the specific causes of seed fate were not followed in this experiment, seed predation by small mammals was also important in both mixed species and fallow forest treatments (Fig. 1A), where only four and six seeds survived to germination in control treatments, respectively. Further, significant differences existed among exclosure treatments within these forest types (Fig. 1B and C), differences that are clearly due to enhanced survivorship within exclosure treatments.

3.2. Seedling survival and sources of mortality

Survival by seedlings without wire mesh protection over the course of this experiment was significantly different among forest types, with 37% of seedlings surviving in *Gilbertiodendron* controls but only 12 and 9% surviving in mixed species and fallow forest controls, respectively (χ^2 randomization test, data from all four sites of each treatment, $p < 0.0000$). However, surviving seedlings within *Gilbertiodendron* forest showed little growth and often only the first two simple leaves developed.

Seedling survival and mortality by the four sources recorded was significantly different among forest types in controls (Fig. 2). Small mammals were responsible for 48% of seedling mortality in fallow forest where predation occurred within the first week. In contrast, small mammals were responsible for only 2 and 5% of seedling mortality in *Gilbertiodendron* and mixed species forest, respectively. Fungal attack was an important source of mortality in both *Gilbertiodendron* (27%) and mixed species forest (28%), whereas it accounted for only 4% of mortality in fallow forest. Insects were responsible for 55% of seedling mortality within mixed species forest but only 28% in *Gilbertiodendron* and 26% in mixed species forest. Drought was responsible for 13% mortality within forest fallow, while no seedlings succumbed to drought in mixed species forest and 7% of mortality within *Gilbertiodendron* forest was attributed to drought.

Marked differences were observed in seedling mortality patterns over time in control plots among the three forest types (Fig. 3). Forty-eight percent of seedlings in the fallow forest

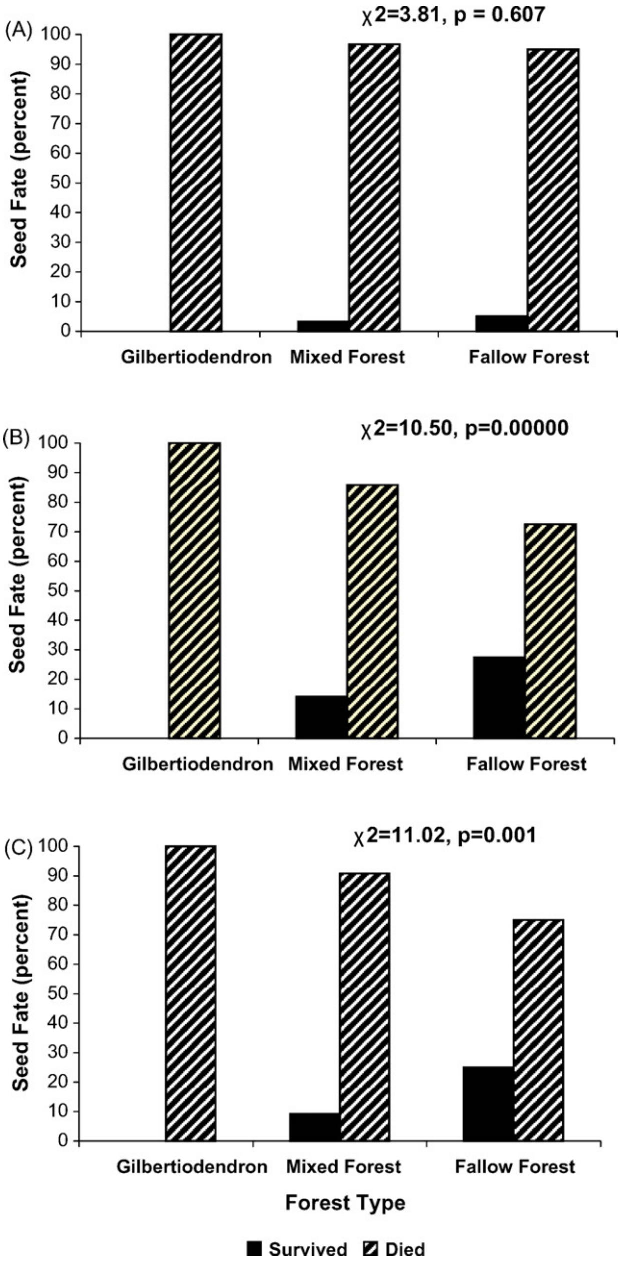

Fig. 1. Seed survival of *Entandrophragma angolense* in *Gilbertiodendron*, mixed species, and fallow forest in the Dzanga-Sangha Dense Forest Reserve, Central African Republic in control without wire mesh cage (A), small opening (B), and large opening (C) mesh cage over 42 days during the wet season. χ2 statistic represents contingency table randomization test of 1000 simulations where "*p*" represents probability value.

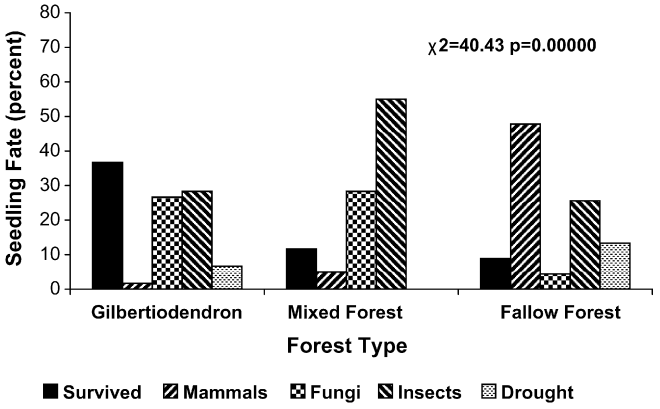

Fig. 2. Seedling survival of *Entandrophragma cylindricum* seedlings in *Gilbertiodendron*, mixed species, and fallow forest in the Dzanga-Sangha Dense Forest Reserve, Central African Republic over 190 days in controls without wire mesh by mortality source. χ2 statistic represents contingency table randomization test of 1000 simulations where "*p*" represents probability value.

died within the first week of the experiment, with little mortality occurring after 4 weeks. In contrast, seedling mortality was high and fairly constant for 6 weeks in mixed species forest, with little mortality after 12 weeks. Finally, seedling mortality was relatively constant during the entire 190 days of observation in *Gilbertiodendron* forest compared to the other forest types. This pattern was consistent with the poor condition of *E. cylindricum* seedlings observed over time in this treatment. Significant differences of seedling survivorship and sources of mortality were observed among exclosure treatments within forest types (Fig. 4A–C). Within both *Gilbertiodendron* and mixed species forest, fungal attack was responsible for higher seedling mortality in the exclosure treatments than in controls. The most pronounced difference, however, was between the control and exclosure treatments within the fallow forest. The elimination of the threat of small mammal predation led to >50% seedling survivorship in each of the exclosure treatments (Fig. 4B).

4. Discussion

4.1. Seed survivorship

The data presented in this study illustrates how the causes of seed mortality can vary with forest type and underscores the importance of small mammals in determining the post-dispersal fate of *E. angolense* seeds (Fig. 1). While seed predation by small mammals can vary by study species and site, seed predation has also been shown to be a significant source of seed mortality for the true mahogany, *Swietenia macrophylla* (Grogan and Galvão, 2006; Norghauer et al., 2006; but see also Gullison et al., 1996).

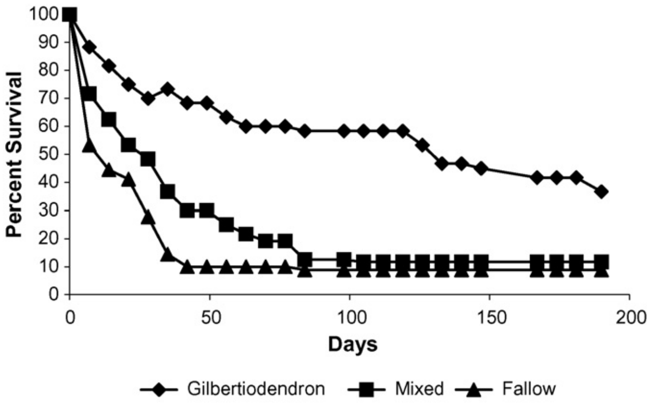

Fig. 3. Percent seedling survival of *Entandrophragma cylindricum* seedlings in *Gilbertiodendron*, mixed species, and fallow forest in the Dzanga-Sangha Dense Forest Reserve, Central African Republic over 190 days in controls without wire mesh.

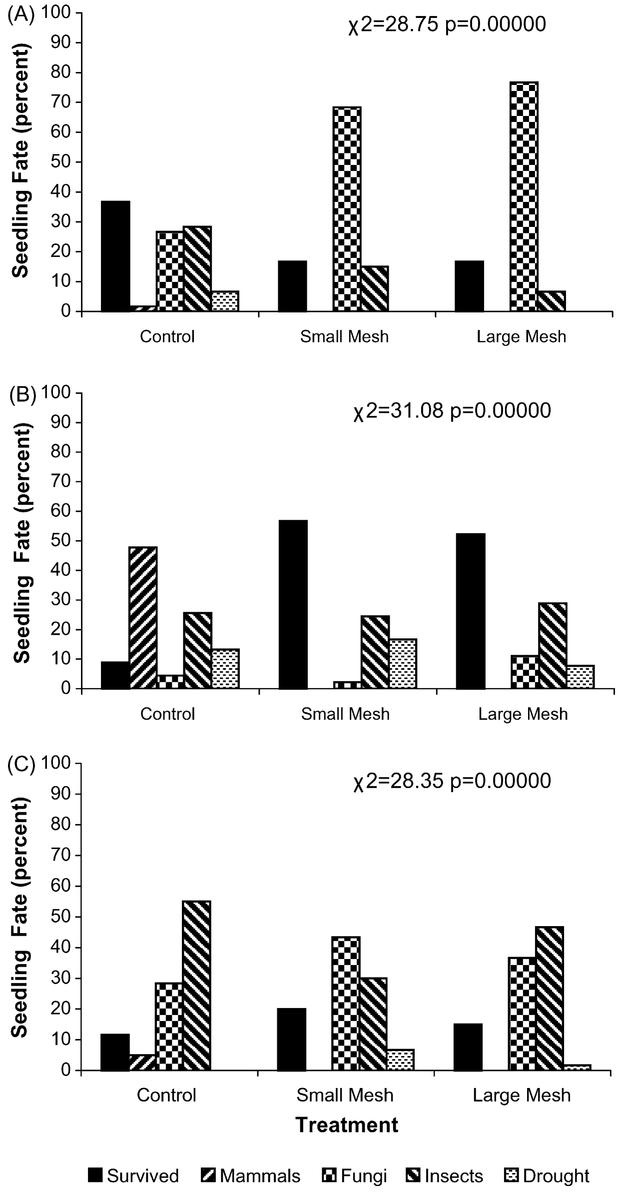

Fig. 4. Seedling survival of *Entandrophragma cylindricum* seedlings in *Gilbertiodendron* (A), fallow (B), and mixed (C) species forest in the Dzanga-Sangha Dense Forest Reserve, Central African Republic over 190 days in control without wire mesh cage, small opening, and large opening mesh cage and by mortality source. $\chi 2$ statistic represents contingency table randomization test of 1000 simulations where "*p*" represents probability value.

Because the small mammals responsible for seed predation here are probably not sufficiently specialized in their diet to distinguish among *Entandrophragma* species (Hammond and Brown, 1998; Norghauer et al., 2006), these results can reasonably be expected to reflect seed predation rates on seeds of congeners found within the study area (Synnott, 1975; Makana and Thomas, 2004). Because exclosures were designed to keep out different size classes of seed predators, a minimum estimate of seed mortality resulting from small mammal predation can be provided by subtracting the percent survivorship in control plots (no wire mesh) from the percent surviving to germination in exclosures. This suggests that predation is responsible for approximately 10 and 25% of seed mortality in mixed species and fallow forest, respectively.

Small mammal seed predators in *Gilbertiodendron* forest managed to break into seedling exclosures and consume all seeds. *Gilbertiodendron dewevrei* is a mast fruiting species that typically produces abundant fruit every 3–7 years. Blake and Fay (1997) noted that in mast years *Gilbertiodendron* produces between 3.76 and 4.73 tonnes (fresh mass) of seeds ha^{-1}, representing a major food source for a wide variety of large and small mammals. Because species richness, stem density, and basal area are low for other tree species in this forest type, it follows that they produce few seeds relative to *Gilbertiodendron*. Data from this study suggests that in non-mast years for *Gilbertiodendron* such as the year of this experiment, food scarcity may be so severe within this forest type that few edible seeds of any species will survive to germination.

4.2. Seedling survivorship

This study addressed the seedling establishment phase from 1-week-old seedlings through 190 days. Within this life phase, *E. cylindricum* seedlings suffered quite different fates in the three forest types studied (Fig. 2). Differences were likely due in part to the influence of forest structure which spans a gradient from dense closed canopy (*Gilbertiodendron* forest) to semi-broken canopy in mixed species forest to very broken canopy in early successional fallow forest. These structural differences lead to different micro-climates within the forest types. Vierling and Wessman (2000) have shown that understory light conditions extend vertically through the forest up to within a few meters of the canopy bottom in *Gilbertiodendron* stands in neighboring Republic of Congo. In contrast, while no data on light quality and quantity exists from mixed species forest within the study area, it is evident that the semi-broken nature of the canopy in combination with multiple treefall gaps leads to a complex light environment across the forest floor. The early successional nature of the fallow forest creates fairly open conditions resulting in relatively abundant light at the ground level. Neither relative humidity nor temperature has been measured in any of these forest types within the study area; however, it is clear from working within these forests that a gradient exists characterized by relatively cool-humid conditions in *Gilbertiodendron* forest, a hot-dry microclimate in the forest fallow understory, and intermediate conditions in mixed species forest (Hall, personal observation).

The different ranking of the sources of seedling mortality observed in this study (Fig. 2) is not surprising given the differences in forest structure and tree species richness described above. The relative importance of fungal attack causing mortality in both *Gilbertiodendron* and mixed species forest is likely the result of the dark and humid understory within these forests. The increased importance of this factor within these forest types with the addition of wire mesh cages (Fig. 4A and C) may result from fallen leaves on the cages creating an even more dark and humid environment within the cages.

Seedling death due to drought was notable in the fallow forest and almost negligible within the other two forest types

(Figs. 2 and 4). As fallow forest is characterized by a low and open canopy, it is not surprising that dry season conditions in these fallow forests would lead to marked seedling death in these early establishment phase seedlings.

Malcolm and Ray (2000) have shown how small mammal assemblages shift as forests are opened up to invasion by savanna species with the introduction of logging roads. In this experiment, both *Gilbertiodendron* and mixed species forest sites were at least 300 m from the nearest road, field, or skidder trail, a distance sufficient to avoid the invasion of savanna and/or disturbance adapted species of small mammals (Ray, personal communication). Thus, it is reasonable to assume that the fallow forest contained a different small mammal community than either of the other two sites and resulted in the increased mortality due to small mammals observed there.

4.3. Applications to forest management

These results provide important guidance to natural forest management of *Entandrophragma* spp. High levels of seedling death recorded in this experiment help explain the disappearance of seedling carpets reported by Hall et al. (2003b) within unlogged mixed species forest and highlight the fact that simply relying on natural processes of dispersal, regeneration, and recruitment to replace harvested trees under natural forest management is problematic. Because of their commercial value, *Entandrophragma* spp. may be among the few species harvested in Central African forests for which outplanting seedlings after logging may be economically justified. However, planting recently germinated *Entandrophragma* seedlings into mixed species forest understory would have little chance of success (Fig. 4). The combination of the high level of insect damage and fungal attack resulting in seedling death in this forest type would thwart such efforts.

Although survival reported here was markedly lower, these results are consistent with those reported by Makana and Thomas (2004) who followed seedlings of *E. utile* and the true African mahogany, *Khaya anthotheca*, within gap and understory treatments in eastern Democratic Republic of Congo. These authors reported 33.3% (gap) and 31.7% (understory) survival for *E. utile* seeds recruiting to seedlings 11 weeks after seed addition. Subsequent recruitment to 18 months was 85% in gaps and 37% in the understory for this species. Inferences drawn from work conducted by Swaine et al. (1997) in Ghana, survival data reported by Makana and Thomas (2004), and on-going research in the Central African Republic (Hall, unpublished data) suggest that planting older seedlings of these species into gaps (accompanied by liberation treatments as necessary) may be a viable strategy to improve stocking in natural forest.

The differences in seed and seedling survivorship between exclosure and control treatments in mixed species and fallow forest suggest that using exclosures would be an effective way to increase survivorship. In areas of high human population density where timber concessions are overtaken by agriculture such as eastern Democratic Republic of Congo (Makana, 2000), encouraging local people to plant Africa mahoganies as part of an agroforestry system may be warranted. However, while exclosures would likely increase seed (in mixed species and fallow forest) and seedling (in fallow forest) survivorship and recruitment, there is a risk that the wire mesh would be stolen (Synnott, 1975; this study).

All of the seedling mortality experienced in the fallow forest seedling control of this experiment due to small mammals (48%) occurred during the first week after outplanting recent germinants. A better alternative to protecting seeds or recent germinants would be to outplant seedlings that have been raised for several months in a nursery. Such seedlings would have overcome this early period of vulnerability to small mammals. Because drought-related seedling mortality is important in fallow forest, a further recommendation would be to outplant seedlings after the end of the dry season. This methodology has been suggested by Debroux (1998) for moabi (*Baillonella toxisperma*) in Cameroon and has also been successfully employed at the Dzanga-Sangha study site.

The seedling survivorship data presented in this experiment for *Gilbertiodendron* forest controls suggests that for the correct species, enrichment planting may be worthy of further investigation. At least two companies within Central Africa – one in Republic of Congo and one in Democratic Republic of Congo – have experimented with and are actively attempting to develop a market for *Gilbertiodendron*. Thus, it is conceivable that *Gilbertiodendron* forest will become actively exploited in the coming years. Given the fact that *Gilbertiodendron* is consistently found on low base cation soils (Guillot, 1981; Hart et al., 1989; Hall et al., unpublished data), species chosen for enrichment planting in *Gilbertiodendron* forest should be those adapted to poor soils. Since *E. candollei* has been shown to be associated with and its seedlings grow relatively well on poor base cation soils (Hall et al., 2003a; 2004) and because it is relatively abundant within *Gilbertiodendron* stands (CTFT, 1985), it would appear to be a good candidate for enrichment planting trials in this forest type.

5. Conclusions

African mahoganies are among the most valuable timber species in Central Africa and in many areas represent the highest export volume. The exceptional value of these species suggests that they are among the best candidates for long-term timber management. One aspect of managing these species for timber production is assuring their regeneration. It is clear from this study that seed mortality is high be it in monodominant *Gilbertiodendron*, mixed, or fallow forest. While seedling mortality was highest in mixed species and fallow forest treatments, important differences in mortality pathways were observed. It appears that the best way to improve timber production in natural forest would be to plant out seedlings from nurseries at the end of the dry season in forest gaps with appropriate soil chemical composition. Agroforestry systems where seedlings are similarly planted out in fallow forest would also appear to have a reasonable probability of success.

Seedling survival in *Gilbertiodendron* forest was unexpectedly high in control treatments. Observations of seedling vigor suggest that should enrichment planting be contemplated here, attention should be paid to species. Given its known association with and ability to grow on poor soils, *E. candollei* would be a logical candidate for outplanting trials within this forest type. Because there is an effort currently underway to sell *Gilbertiodendron* on the global market, enrichment planting of *E. candollei* within this forest type may become an attractive management option in logged forest.

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