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Effects of Termites *(Macrotermes)* and Large Herbivores on Exotic and Native Tree Species in Lake Mburo National Park, Uganda

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ABSTRACT

Both termites and large herbivores are important to ecological processes in the African savannah. Termites and large herbivores contribute to spatial heterogeneity in distinct ways. Large herbivores facilitate tree regeneration through feeding preferences, thereby causing reduced competition between grasses and woody plants. Herbivores also act as predators on tree seedlings, thus reducing seedling growth and survival. Termites of the genus *Macrotermes* are considered pests in plantation sites, although they also act as ecosystem engineers through their rearrangements of soil layers and nutrient-rich termite mounds (termitaria). This study focused on the effects of termites and large ungulates on growth and survival of both native and exotic seedlings in Lake Mburo National Park, Uganda. A total of 720 seedlings representing four different species were planted and measured in open and fenced plots, controlling the access of large herbivores. Within each plot, five individuals of each species were either covered with a netted basket or uncovered, thus unprotected from termite attacks. Treatments were replicated at nine different sites throughout the park. Termites were observed *in situ* biting off seedling stems, as well as by holes and disturbances on the top soil layer. Herbivore activity was observed within sites in the form of dung, clay and scrape markings on the ground. Exclusion of large herbivores had a positive effect on seeding growth rate and seedling survival. All four species had highest growth rates when protected from both herbivores and termites, and *Eucalyptus grandis* grew taller than any of the other tree species. The exotic seedlings had higher survival rates compared to the indigenous seedlings. Termites had an additional small negative effect on seedling growth when combined with herbivore browsing. Termites also negatively affected native seedlings by reducing survival to 20% in plots where both large herbivores and termites accessed the seedlings. Termites had little impact on the survival of exotic species. Based on these results, I suggest that predation of large herbivores and termites on seedlings have a negative effect on tree regeneration in Lake Mburo National Park. The negative effect of termites on indigenous seedlings is probably a result of joint effects of termite preferences and herbivore activity, as termite impact on seedlings are only seen when combined with the influence of large herbivores.

SAMMENDRAG

Både termitter og store herbivorer er viktige funksjonelle grupper på den afrikanske savannen. Termitter og store herbivorer bidrar til romlig heterogenitet på ulike måter. Store herbivorer tilrettelegger regenerasjon av planter og trær gjennom deres beitepreferanser, noe som gir redusert konkurranse mellom gress og annen vegetasjon. Herbivorer er også predatorer på unge trær, og bidrar dermed til redusert vekst og overlevelse av disse. Termitter innenfor slekten *Macrotermes* blir sett på som en pest, spesielt i sammenheng med plantasjer, men de er også viktige bidragsytere i økosystemet gjennom å omarrangere jordlag og konstruksjon av næringsrike termittuer (termitaria). Denne studien fokuserte på effektene av termitter og store herbivorer på vekst og overlevelse av både naturlig forekommende og eksotiske unge trær (<1 år) i Lake Mburo National Park, Uganda. Totalt 720 unge trær av fire ulike arter ble plantet og målt i åpne og inngjerdete soner, som gjorde plantene utilgjengelig for herbivorene. Innenfor hver sone var det fem individer av hver art som var enten tildekket med beskyttende kurver eller ikke for å kontrollere termitters tilgjengelighet til plantene. Behandlingene ble gjentatt ved ni ulike beliggenheter i parken. Termitter ble observert *in situ* mens de bet av stammen på de unge trærne, og ved dannelse av hull og andre forstyrrelser i det øverste jordlaget. Herbivoraktivitet ble observert i form av ekskrementer, samt leire- og skrapespor på bakken og gjerder. Ekskludering av store herbivorer hadde en positiv effekt på vekst og overlevelse av unge trær. Alle fire arter hadde høyest vekstrate når de var beskyttet fra både termitter og herbivorer, og *Eucalyptus grandis* vokste seg høyest av alle. De eksotiske artene hadde lavere sannsynlighet for å dø sammenlignet med de naturlig forekommende artene. Termitter hadde en liten negativ additiv effekt på vekstrate når de ble kombinert med beiting av store herbivorer. Termitter påvirket også innfødte arter negativt ved å redusere overlevelse med 20% i soner med både termitter og herbivorer. Termitter hadde liten innflytelse på overlevelse av eksotiske arter. Basert på disse resultatene foreslår jeg at predasjon av store herbivorer og termitter på unge trær har en negativ påvirkning på treregenerasjon i Lake Mburo National Park. Den negative effekten termitter har på naturlig forekommende unge trær er sannsynligvis et resultat av sammenføyde effekter av termittpreferanser og herbivoraktivitet, fordi termitters innvirkning på plantene kun sees når de kombineres med effekter av store herbivorer.

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1. INTRODUCTION

Termite mounds (termitaria) are a characteristic feature of the African savannah, and important to the ecological processes that comprise the savannah ecosystems (Eggleton *et al.* 1996; Junqueira *et al.* 2008). Termites are represented by a vast number of species and variable feeding strategies (Lee & Wood 1971), but they generally decompose and rearrange soil layers through underground tunnel structures, thereby increasing water, air and mineral flow (Jouquet *et al.* 2011). Termites belonging to the genus *Macrotermes* (family Termitidae; subfamily Macrotermitinae) act as ecosystem engineers by changing the surrounding environment and creating different conditions than adjacent soil (Gosling *et al.* 2012; Okullo & Moe 2012; Traoré *et al.* 2008;). Their so-called allogenic engineering transforms organic and mineral materials from one state to another by altering soil hydrology and drainage (Jones *et al.* 1994). Such conditions contribute to savannah spatial heterogeneity by supporting a large number of plant species on nutrient-rich *Macrotermes* mounds (Fox-Dobbs *et al.* 2010; Loveridge & Moe 2004; Moe *et al.* 2009a; Sileshi *et al.* 2010). Dangerfield *et al.* (1998) found that the species *Macrotermes michaelseni* not only works as an ecosystem engineer through various feedback mechanisms, but *M. michaelseni* also affects plant growth positively through increased availability of resources. This result is supported by previous findings by Watson (1977), who concluded that *Macrotermes falciger* mounds greatly induced crop production due to soil nutrient availability. More recently, Moe *et al.* (2009a) found that the termite *Macrotermes herus* increased savannah heterogeneity through their mound-building and plant species enrichment. Thus, *Macrotermes* are of great importance as ecosystem engineers, agents of soil enrichment and plant diversity.

Nevertheless, termites are generally considered a pest in many agricultural and plantation sites because of their woody diet (Cowie *et al.* 1989; Ssemaganda *et al.* 2011). Termites of various functional groups have caused severe damage to plantations and other commercial forests (Junqueira *et al.* 2008). More specifically are *Macrotermes* considered to be among the most destructive, in particular where exotic tree species are planted (Cowie *et al.* 1989). Contrary to several other termite subfamilies, Macrotermitinae do not have the necessary components in their digestive system to break down the strong cellulose building blocks of plant cell walls, and instead grow fungi within their mound compound (Schuurman 2005). These fungi (genus *Termitomyces)* feed on the cellulose of plant cell membranes, thus relocating organic material and increasing soil nutrients. This seemingly mutualistic relationship between the termites and fungi is what may reduce wood products considerably by damaging plant structure and viability (Ssemaganda *et al.* 2011). Such an obligate symbiosis also makes it possible for the termites to decompose wood litter at higher rates than other non-fungus-growing species, because their digestive system is not restricted to the termite body itself (Schuurman 2005). *Macrotermes* attacks on trees may therefore have profound economic impacts on local plantations, and are consequently subject to various control measurements.

Pest management practices vary according to the purpose of trees planted. Some trees are combined with other crop or tree species, such as in agroforestry or multipurpose systems. These are subject to control measures often developed by local farmers, such as physically destroying the termite mound and its queen or applying meat, ash or crushed fruits into planting holes (Sileshi *et al.* 2008). Other trees are planted on a larger scale, often giving preventive measures that affect larger areas. Such control activities include using cyclodienes, a liquid and persistent pesticide used directly around the planted tree or as poison on the termite mound (Cowie *et al.* 1989). However, as noted by Cowie *et al.* (1989) as well as Logan *et al.* (1990), non-chemical preventives provide the most promising long-term solution to termite attacks, and suggest any alternative strategy to avoid chemical pollution should involve planting tolerant, resistant or indigenous tree species.

Eucalyptus trees are commonly used as plantation species throughout Africa, although their susceptibility to termite attacks is generally very high (Atkinson *et al.* 1992; Ssemaganda *et al.* 2011). In Uganda, *Eucalyptus grandis* is the most widespread commercial and constructional plant species (Ssemaganda *et al.* 2011). Atkinson *et al.* (1992) found that this was also among the least tolerable of several *Eucalyptus* species when attacked by *Macrotermes natalensis*. However, *E. grandis* from Zimbabwe was more tolerant than the same species from South Africa, possibly as a result of long-term termite attacks and selection for termite tolerance. Furthermore, Atkinson *et al.* (1992) noted that termite damage on Eucalypt trees planted in Africa was not equivalent to the damage occurring where the trees originated. This was explained by the different age classes of the trees at the time when termite attacks took place. In Africa, most trees are attacked when they are young seedlings, and resistance to termite damage at an older age gives little protection for young trees (Atkinson *et al.* 1992).

In addition to termites, also large herbivores have profound effects on the structure of their environment (Hobbs 1996; Okullo & Moe 2012). Both domestic and wild herbivores affect plant regeneration, *i.e.* the survival and growth of plant seedlings, in numerous ways. They may decrease seedling survival (Sharam *et al.* 2006) or plant growth (Augustine & McNaughton 2004; Midgley *et al.* 2010) directly through predation, or facilitate seedling regeneration indirectly through interspecific competition between woody plants alone (Riginos & Young 2007) or between grasses and tree seedlings (Davis *et al.* 1998; Riginos 2009) by reducing plant species preferred by herbivores. Although there are many factors determining whether herbivores, large and medium sized, have a positive or negative effect on their surroundings, it is well established that browsers negatively influence woody seedling survival (Belsky 1984; Moe *et al.* 2009b; Prins & van der Jeugd 1993). For instance, O'Kane *et al.* (2012) found that density of the impala *(Aepyceros melampus)* was inversely correlated with the density of woody plants. The impala was also the probable cause of decreased seedling survival in a study provided by Moe *et al.* (2009b), suggesting the importance of browsers in landscape dynamics. Sharam *et al.* (2006) showed that exclusion of browsers increased seedling survival by 70 percent. Browsers also limited tree recruitment by reducing seedling growth, thus affecting even pioneer species (Sharam *et al.* 2006). High browsing pressure may in fact lead to even-aged stands where tree establishment is commonly only allowed by removal of herbivores through diseases or poaching (Caughley 1976; Prins & van der Jeugd 1993). Even though browsing may have an immediate negative effect on plant growth or survival, the same factors may also favour seedling regeneration with time. Davis *et al.* (1998) concluded that increased water available for seedlings had a strong positive influence on seedling regeneration. This could be a consequence of grazing, which decreases competition for soil water between woody seedlings or other vegetation (McNaughton 1983; Walker *et al*. 1981). Thus, herbivores may determine landscape dynamics based on seedling preferences and favourable feeding grounds.

Attracted by its relatively unique and high plant species diversity, large herbivores use termitaria as feeding grounds in an otherwise rather scarce savannah landscape (Levick *et al.* 2010; Mobæk *et al.* 2005; Seymour *et al.* 2014). Loveridge & Moe (2004) suggested the important nutritional value of termitaria vegetation, functioning as browsing hotspots in a nutrient-poor environment. In addition, Traoré *et al.* (2008) found an increased species richness as well as plant density surrounding the *Macrotermes* mounds suggesting that the large mammals visiting these vegetative hotspots also affect their surroundings by remaining near the mound structure. The herbivores who are attracted to the nutrient-rich vegetation may therefore also add nutrition in terms of dung and urine (Brody *et al.* 2010; Sileshi *et al.* 2010).

As termitaria are common in African savannahs, large herbivores should also impact seedling regeneration in combination with termite activity. This experiment has therefore combined the effects of termites on both exotic and native tree species as well as considered the potential role of large herbivores.

The objectives of this study was to investigate how termites of the genus *Macrotermes* and large ungulates affect seedling mortality rates and growth rates of native as well as exotic species. Exotic species are more susceptible to termite and ungulate feeding since native trees are more adapted to local insect and ungulate fauna. Therefore, I predicted that the exotic species would be more susceptible to termite attacks than native plant species, leading to a higher mortality rate among the exotic seedlings compared to the indigenous seedlings. I predicted that the exotic species would grow faster than native species because exotic species are selected based on their fast growth rates. I also expected large herbivores to have a negative effect on seedling growth rates, possibly due to stress from termite attacks.

2. METHODS

2.1 Study site

Lake Mburo National Park lies in the south-west of Uganda, and covers about 260 km^2. Its equatorial location (between $00^o30´$-$00^o45´$S and $45^o00´$-$31^o05´$E) indicates no clear seasonal changes in temperatures, with an average annual temperature at 27.5^oC (Bloesch 2002). However, there are generally two rainy seasons, the long rains from October to December and the short rains from February to June. Average annual rainfall in the park is approximately 800 mm (Bloesch 2002). The study area is located in the Northern Kagera region, and the park is part of the Lake Mburo ecosystem which consists of the protected park and surrounding privately and government owned land containing agricultural crops and livestock. The vegetation composition is divided into areas of dry savannah, thickets, woodland and swamps. There are five lakes within the park contributing to wetlands, coherent with valley swamps and the Rwizi river. The landscape is dominated by *Acacia* species, and the most common is *Acacia hockii* (Moe *et al.* 2009a). The most common soil types in the park are ferralsols, histosols, leptosols and vertisols, all of medium to fine texture with relatively high clay contents (Bloesch 2002). The study sites are situated in eastern and western valleys within the park, where large termite mounds covered with thicket vegetation interrupt the savannah landscape.

Lake Mburo National Park supports several wild ungulate species, with impala *(Aepyceros melampus)*, zebra *(Equus burchelli)*, waterbuck *(Kobus ellipsiprymnus defassa)* (Rannestad *et al.* 2006) as well as the smaller warthog *(Phacochoerus africanus)* (Moe *et al.* 2009a) being well represented in terms of numbers. Most large mounds in Uganda are built by termites of the genus *Macrotermes* (Pomeroy 1977), and the most common termite species within the park is *Macrotermes herus*, a fungus-growing and mound-building termite often noticed by its termitaria constructions (Bakuneeta 1989). Although the genus *Macrotermes* is well represented in terms of numbers, there are also numerous other termite species within this park.

2.2 Experimental tree species

2.2.1 Exotics

Eucalyptus grandis is one of the most common plantation species used in the tropics (Jacovelli *et al.* 2009). It plays a significant role in the tropical timber industry, mainly because of its ability to grow quickly, thereby outcompeting any other well adapted indigenous trees. *E. grandis* is also a pioneer species, thus making it ideal for plantation purposes because of its ability to grow under various conditions.

Grevillea robusta is a fast growing, deciduous tree preferring soils of medium texture. Although *G. robusta* is not as widely spread as *E. grandis*, this tree could prove valuable as a plantation species because it is also able to grow fast under various soil and elevation conditions. *G. robusta* grows rapidly if planted in suitable sites, but may show signs of stress and die if planted in areas that are too dry (Jacovelli *et al.* 2009).

Both species originate from Australia, but are widely spread throughout African plantations and through other human-induced measures (Ssemaganda *et al.* 2011; Tumwebaze *et al.* 2012).

2.2.2 Natives

Milicia exelsea is a pioneer species that reaches its highest growth potential at moderately high light levels, and is considered an important timber species across Africa (Nichols *et al.* 1998). However, this species is prone to gall attack by plant lice often causing seedling mortality, which in turn leads to a low turnover rate. *M. exelsea* may therefore not be as profitable as other fast growing trees such as *E. grandis* or *G. robusta.*

Maesopsis eminii is a light demanding semi-deciduous tree requiring slightly more fertile soil to reach its maximum height, but it is also a flexible species that can grow under various soil conditions. Because of its dense crown, *M. eminii* has a tendency to outcompete other crops when planted as a multipurpose tree (Okorio *et al.* 1994; Wajja-Musukwe *et al.* 2008). Despite this, *M. eminii* is considered one of the few fast growing indigenous trees in Africa, and is therefore a promising timber species (Buchholz *et al.* 2010; Jacovelli *et al.* 2009). Because this is a native tree it is likely to have evolved some kind of defences against well-known pests, such as termites, fungi and other insects, and may not face the same difficulties as do exotic tree species when planted for commercial purposes.

Both species are found on Ugandan soil, as planted by humans and occurring naturally (Tumwebaze e*t al.* 2012), and are often used for various wooden products, such as furniture and building materials (Sseremba *et al.* 2011). These trees have a wide potential distribution range within Uganda (**Figure 1**), and could be an interesting, and possibly less costly, alternative to exotic plantation species such as *E. grandis* and *G. robusta*.

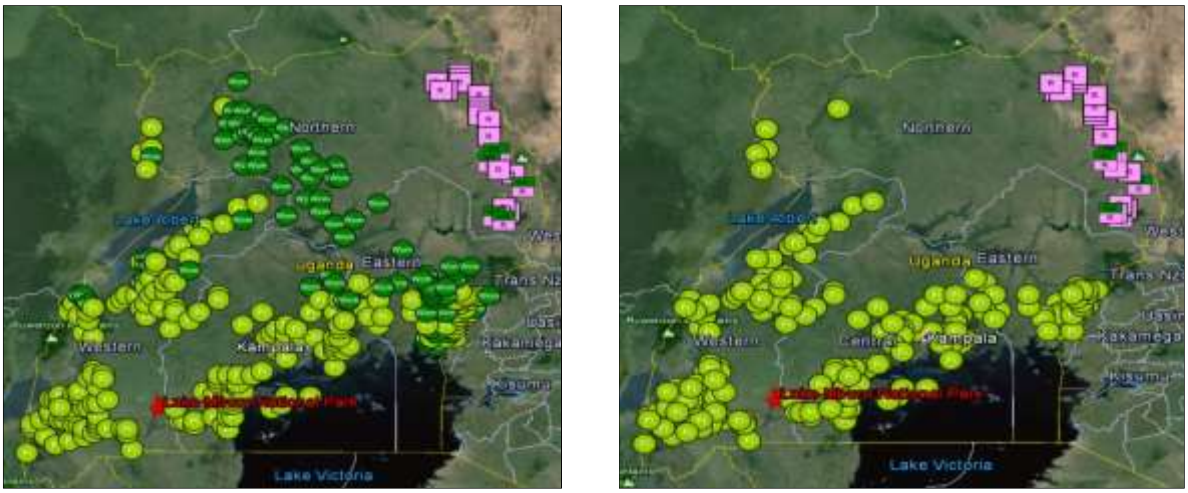

Figure 1. Maps showing potential distribution of *Maesopsis eminii* (left) and *Milicia exelsea* (right) within Uganda. Colours and shapes of markings indicate various vegetation types, such as riverine forests (pink squares), Lake Victoria semi-deciduous rain forest (light green circles) and moist combretum wooded grassland (dark green circles) (van Breugel *et al.* 2012).

2.3 Experimental design

Seedlings (n=720) were planted in nine different sites across three regions of the park. Plot sizes varied from 90-260 m^2, but were always the same size at the same site. Within each site there were two plots, one fenced where no large herbivores could access the seedlings and one open plot where herbivores had free access. In each plot I planted 40 seedlings distributed in four squared zones. Twenty of the seedlings were covered with netted baskets on the ground protecting them from termite attacks, whereas the remaining 20 seedlings were uncovered, thus giving termites free access. The four species were represented in multiples of five individual seedlings undergoing the same treatment within each plot. The seedlings were randomly drawn, and placed on a site map illustrating species, replicate number and termite accessibility before planting occurred (**Figure 2**).

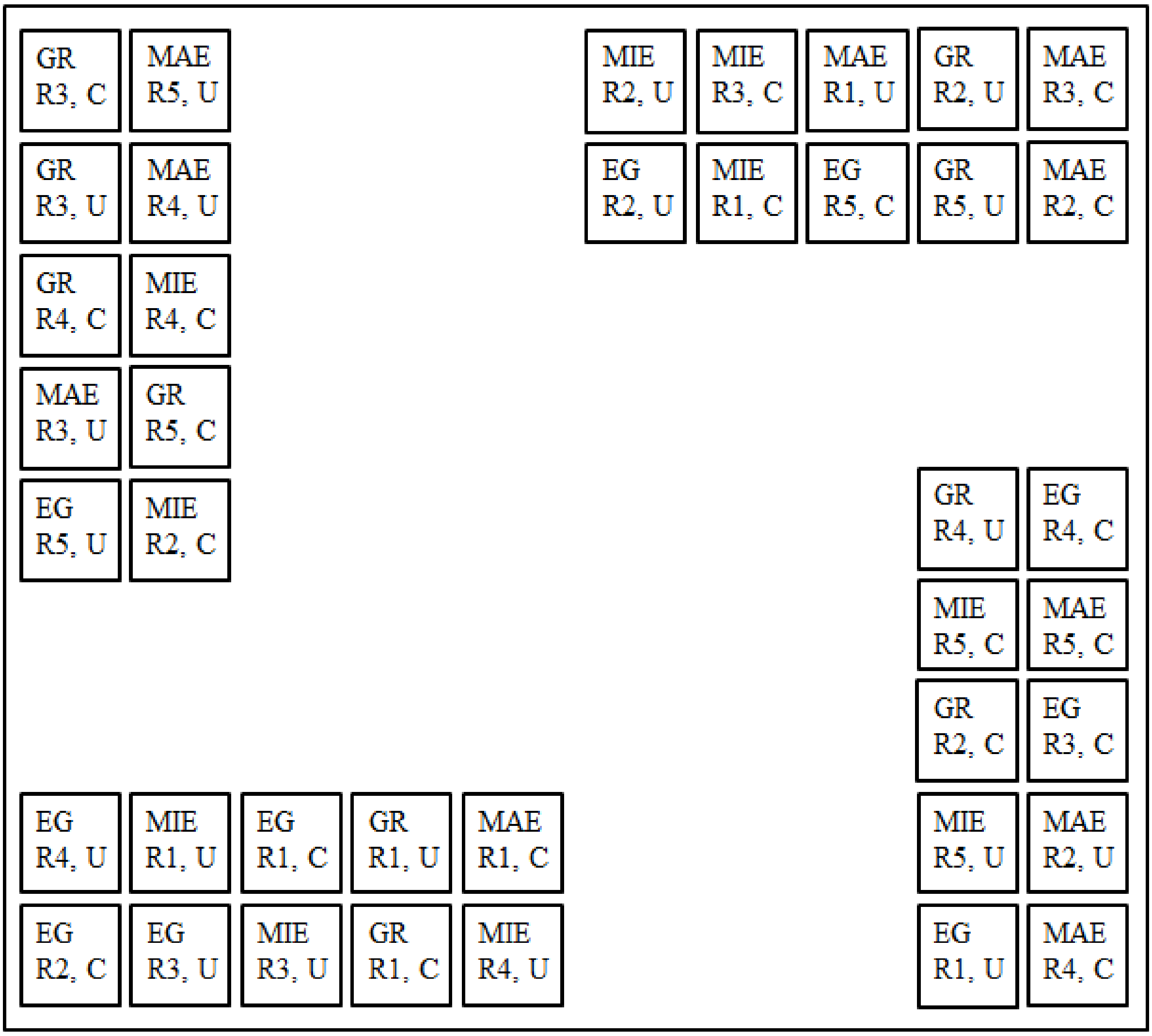

Figure 2. Example of map from the Nshara region of Lake Mburo National Park. The same system was used on fenced and open plots at the same site. Abbreviations: GR *(Grevillea robusta)*, MAE *(Maesopsis eminii)*, MIE *(Milicia exelsea)*, EG *(Eucalyptus grandis)*, R (replicate), C (covered) and U (uncovered).

2.4 Data collection

The data was collected from June to August 2012, and re-sampled in January 2013.

2.4.1 Seedling mortality and growth

The data recorded for each individual seedling were species, site, replicate number, fenced (yes/no), covered (yes/no), dead or alive as well as plant height. All plants were alive when planted.

2.4.2 Termite and herbivore activity

Termite activity was observed *in situ* by holes or tunnels in the soil, and by termites biting off the seedling stem when the dead seedling was picked up, thus leaving the seedling exposed (**Figure 3**). The number of termite mounds within ten meters in each direction of the plots was recorded. The mounds were labelled as active or dormant by digging holes on the outer structure, and then observing the presence of *Macrotermes* soldiers defending their territory.

Figure 3. Termite soil activity within the Sanga region of Lake Mburo National Park (left), and on one of the *Eucalyptus grandis* seedlings within the same region of the park (right).

The activity of large ungulates was recorded as impact on seedling stem and leaves when browsed upon. This was recorded whenever there were clear signs that the seedlings had been browsed, such as where all leaves were removed from the plant or removal of the apical bud, including parts of the stem (**Figure 4)**.

Figure 4. Herbivore browsing on *Grevillea robusta*, which has removed the top parts of the plant, thus reducing seedling height compared to the same species not exposed to herbivore browsing (inset). Both pictures were taken in the Warukiri region of Lake Mburo National Park.

2.5 Statistical analysis

Statistical analysis was done using the statistical program R® version 3.0.2 for Windows. Linear models were used when testing for effects of termite and herbivore activity on seedling survival and height (**Table 1**). Mixed-effects models were used (Crawley 2007), and replicates within each site were treated as pseudoreplicates because of their correlation in both space and time (Hurlbert 1984). In this study, the random effects consist of each plot replicated within sites, while the fixed effects make up the differences between sites (Bolker *et al.* 2008).

Table 1. Response and explanatory variables used when testing for effects of termite and herbivore activity on seedlings.

Response variables	Explanatory Variables
Alive (yes/no)	Covered (yes/no)
Height (cm)	Fenced (yes/no)
	Species
	Site
	Week

A generalized linear mixed model (GLMM) with the binomial response variable dead (1) or alive (0) of seedlings in a given week was used when testing for plant mortality. The GLMM was fitted with the function “glmer” from the R package “lme4” (Bates *et al.* 2014).). A complex model was the starting point for model selection using the function “dredge” in the R package “MuMIn”, resulting in a simpler and more suitable GLMM (Barton 2013). Survival was analysed over three time periods: 1) Overall mortality, 2) Mortality during first period (from June to August) and 3) Mortality between first and second period (from September to December), thus resulting in three GLMMs for seedling survival. The fixed effects included in the GLMMs were Fenced, Species and Covered, the two-way interactions Fenced:Species, Fenced:Covered and Species:Covered as well as the three-way interaction Fenced:Species:Covered. As random effects I fitted random intercepts for each Species nested in Site.

A linear mixed-effects model (LMEM) with the continuous response variable log Height of seedlings was used when testing for plant growth. The LMEM was fitted with the function “lme” from the R package “nlme” (Pinheiro & Bates 2000). The LMEM was also a result of model selection using the same R package as the GLMMs (Barton 2013). Included in this model were the fixed effects Fenced, Species, Covered and Week, the two-way interactions Fenced:Species, Fenced:Week, Fenced:Covered, Species:Week, Species:Covered and Covered:Week as well as the three-way interactions Fenced:Species:Week, Fenced:Species:Covered and Species:Covered:Week. As random effects I fitted random slopes in growth per PlantID, nested within Species and Site.

3. RESULTS

3.1 Seedling mortality

Inclusion of large mammals increased total mortality rates in all four species (**Table 2**, **Figure 5**). The two indigenous species *Milicia exelsea* and *Maesopsis eminii* showed highest probability of dying when planted in open plots with no cover, leaving access to both herbivores and termites. Their chances of survival were thus highest when completely protected. *M. exelsea* had 80% chance of dying when attacked by both termites and herbivores, which was reduced to 60% when browsed by herbivores alone. In contrast, *Eucalyptus grandis* and *Grevillea robusta* had lowest probability of dying when herbivores were excluded but not termites. Their mortality rates were thus highest when unprotected from herbivores alone. About 25% of *G. robusta* seedlings died, which is the lowest mortality of all species in this experiment (**Figure 6**).

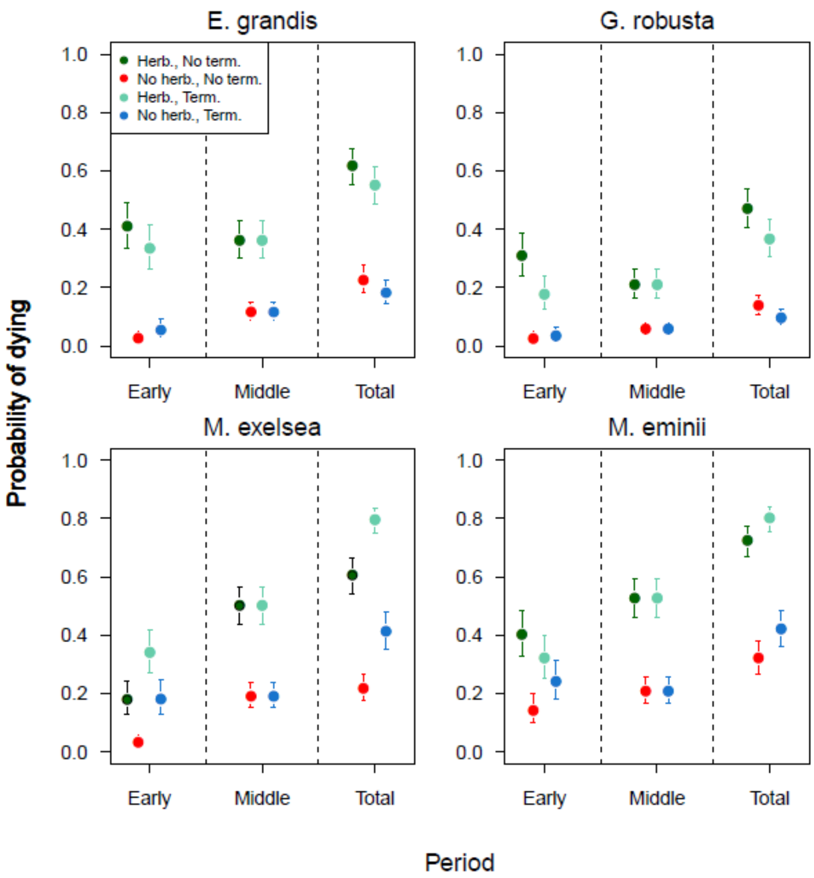

Figure 5. Seedling mortality probabilities in *Eucalyptus grandis, Grevillea robusta, Milicia exelsea* and *Maesopsis eminii*, Lake Mburo National Park. The presence or absence of herbivores and termites is labelled by “Herb” or ”No herb.” and “Term” or ”No term.”, respectfully. The figure is based on predictions from the most parsimonious models given in Table 2.

Table 2. Seedling mortality estimates when using three generalized linear mixed models (GLMMs). The GLMMs are divided into three time periods: 1) Overall mortality, 2) Mortality during first period and 3) Mortality between first and second period. Abbreviations: G.rob *(Grevillea robusta)*, E.gra *(Eucalyptus grandis)*, M.emi *(Maesopsis eminii)* and M.exe *(Milicia exelsea)*.

Overall mortality				
Fixed effects:				
	Estimate	SE	z	p
Intercept	0.20	0.26	0.78	0.438
Fenced (yes vs no)	-1.71	0.17	-9.81	<0.001
Species (G.rob vs E.gra)	-0.74	0.36	-2.08	0.038
Species (M.emi vs E.gra)	1.20	0.34	3.52	0.000
Species (M.exe vs E.gra)	1.17	0.34	3.43	0.001
Covered (yes vs no)	0.28	0.33	0.83	0.405
Species (G.rob vs E.gra) x Covered (yes vs no)	0.15	0.49	0.30	0.767
Species (M.emi vs E.gra) x Covered (yes vs no)	-0.71	0.47	-1.52	0.129
Species (M.exe vs E.gra) x Covered (yes vs no)	-1.22	0.47	-2.59	0.010
Random effects:				
Groups	Name	Variance	SD	
Species x Site	(Intercept)	0.01	0.10	
Site	(Intercept)	0.05	0.23	

Mortality during first period (up to week 10)				
Fixed effects:				
	Estimate	SE	z	p
Intercept	-0.68	0.34	-2	0.046
Fenced (yes vs no)	-2.18	0.60	-3.65	0.000
Species (G.rob vs E.gra)	-0.86	0.48	-1.79	0.074
Species (M.emi vs E.gra)	-0.07	0.43	-0.16	0.877
Species (M.exe vs E.gra)	0.02	0.43	0.06	0.956
Covered (yes vs no)	0.32	0.42	0.78	0.437
Fenced (yes vs no) x Covered (yes vs no)	-1.02	0.49	-2.09	0.036
Species (G.rob vs E.gra) x Covered (yes vs no)	0.41	0.62	0.66	0.509
Species (M.emi vs E.gra) x Covered (yes vs no)	0.03	0.55	0.06	0.956
Species (M.exe vs E.gra) x Covered (yes vs no)	-1.19	0.60	-1.98	0.047
Fenced (yes vs no) x Species (G.rob vs E.gra)	0.40	0.86	0.46	0.645
Fenced (yes vs. no) x Species (M.emi vs E.gra)	1.79	0.67	2.67	0.008
Fenced (yes vs no) x Species (M.exe vs E.gra)	1.34	0.72	1.85	0.064
Random effects:				
Groups	Name	Variance	SD	
Species x Site	(Intercept)	0	0	
Site	(Intercept)	0.19	0.44	

Mortality between first and second period				
Fixed effects:				
	Estimate	SE	z	p
Intercept	-0.57	0.28	-2.06	0.040
Fenced (yes vs no)	-1.45	0.22	-6.75	<0.001
Species (G.rob vs E.gra)	-0.76	0.33	-2.31	0.021
Species (M.emi vs E.gra)	0.68	0.29	2.33	0.02
Species (M.exe vs E.gra)	0.58	0.29	2.02	0.043
Random effects:				
Groups	Name	Variance	SD	
Species x Site	(Intercept)	0	0	
Site	(Intercept)	0.20	0.44	

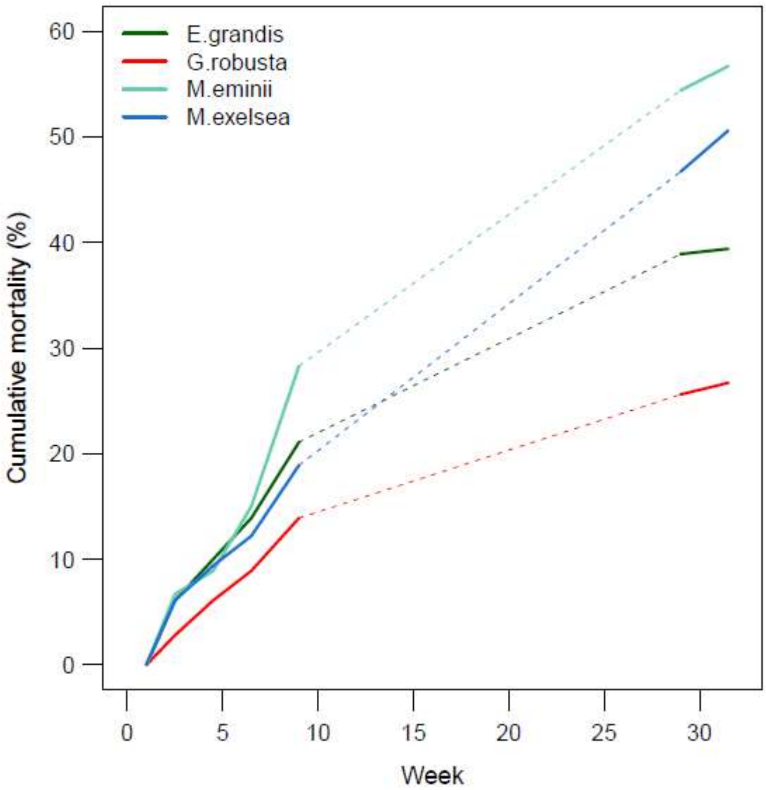

Figure 6. Total cumulative mortality in *Eucalyptus grandis*, *Grevillea robusta*, *Milicia exelsea* and *Maesopsis eminii*, Lake Mburo National Park. The graph shows death frequencies alone, and does not take into account treatment and effects of surrounding animals.

3.2 Seedling growth

Exclusion of large herbivores increased growth rates for all species substantially, while protection from termites only had a marginally additional positive effect on seedling growth (cm) in both open and fenced plots (**Table 3**, **Figure 7**). The exotic species *Eucalyptus grandis* grew faster than any of the other species regardless of treatment, and the two indigenous species *Milicia exelsea* and *Maesopsis eminii*, had relatively low growth rates compared to *E. grandis* and *Grevillea robusta*.

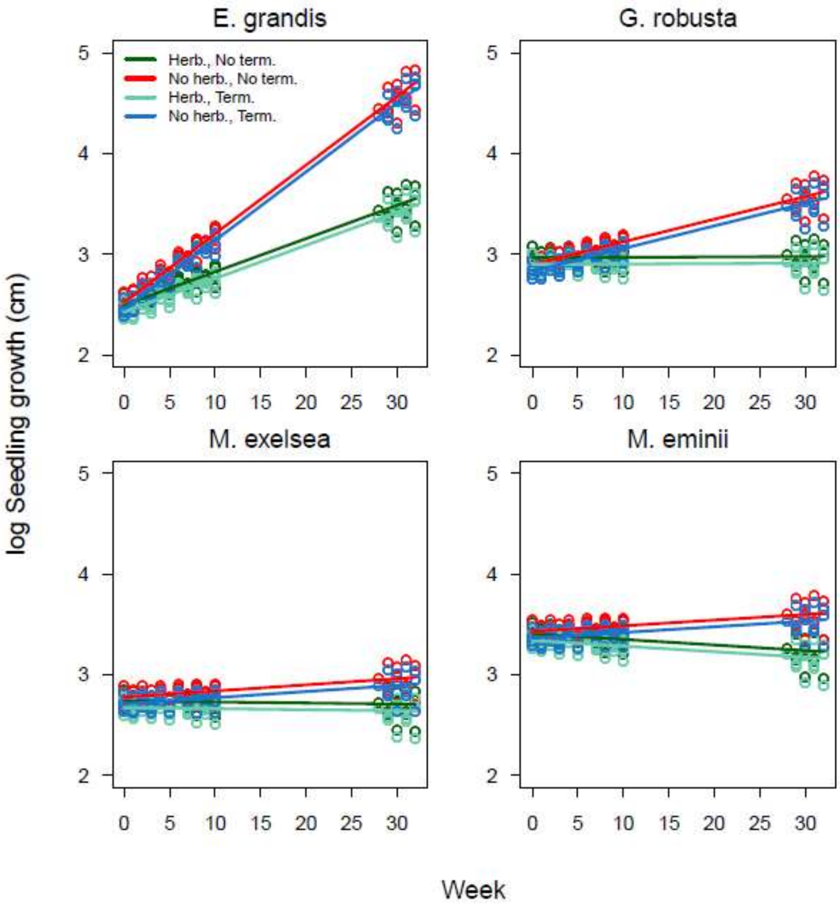

Figure 7. Logarithmic seedling growth (cm) in *Eucalyptus grandis*, *Grevillea robusta*, *Milicia exelsea* and *Maesopsis eminii*, Lake Mburo National Park. The presence or absence of herbivores and termites is labelled by "Herb" or "No herb." and "Term" or "No term.", respectfully. The figure is based on predictions from the most parsimonious models given in Table 3.

Table 3. Seedling growth estimates when using a linear mixed-effects model (LMEM). Abbreviations: G.rob *(Grevillea robusta)*, E.gra *(Eucalyptus grandis)*, M.emi *(Maesopsis eminii)* and M.exe *(Milicia exelsea)*,

Seedling growth					
Fixed effects:					
	Estimate	SE	DF	t	p
Intercept	2.43	0.04	3326	58.85	<0.001
Fenced (yes vs no)	0.03	0.04	679	0.65	0.514
Species (G.rob vs E.gra)	0.47	0.04	24	11.08	<0.001
Species (M.emi vs E.gra)	0.91	0.04	24	21.19	<0.001
Species (M.exe vs E.gra)	0.24	0.04	24	5.68	0.001
Covered (yes vs no)	0.07	0.02	679	3.56	0.000
Week	0.03	0.00	3326	11.26	<0.001
Fenced (yes vs no) x Species (G.rob vs E.gra)	-0.09	0.06	679	-1.64	0.102
Fenced (yes vs no) x Species (M.emi vs E.gra)	0.00	0.06	679	-0.05	0.958
Fenced (yes vs no) x Species (M.exe vs E.gra)	0.01	0.06	679	0.19	0.850
Fenced (yes vs no) x Week	0.04	0.00	3326	11.25	<0.001
Species (G.rob vs E.gra) x Week	-0.03	0.00	3326	-9.88	<0.001
Species (M.emi vs E.gra) x Week	-0.04	0.00	3326	-10.62	<0.001
Species (M.exe vs E.gra) x Week	-0.03	0.00	3326	-9.65	<0.001
Fenced (yes vs no) x Species (G.rob vs E.gra) x Week	-0.01	0.00	3326	-3.10	0.002
Fenced (yes vs no) x Species (M.emi vs E.gra) x Week	-0.02	0.00	3326	-5.21	<0.001
Fenced (yes vs no) x Species (M.exe vs E.gra) x Week	-0.03	0.00	3326	-6.25	<0.001
Random effects:					
Formula: ~Week | Site	SD	Correlation			
Intercept	0.08	(Intr)			
Week	0.00	-0.28			
Formula: ~Week | Species / Site	SD	Correlation			
Intercept	0.02	(Intr)			
Week	0	0			
Formula: ~Week | PlantID / Species / Site	SD	Correlation			
Intercept	0.25	(Intr)			
Week	0.02	-0.34			
Residual	0.17				

4. DISCUSSION

Termites had a negative impact on the survival of native species, in particular *Milicia exelsea*, but not on the exotics. This is in contrast to the assumption that termites greatly reduce seedling survival on exotic timber species rather than indigenous trees (Lee & Wood 1971). The decreased survival rates in indigenous seedlings caused by termites could be explained in various ways. Firstly, it is possible that the termites were selectively killing seedlings, and showed preferences towards the native species when presented with an alternative to exotics. For instance, Gould *et al.* (1993) found that termites did considerable damage to indigenous species in a Tanzanian semi-deciduous forest. In addition, the termites may have possessed a feeding preference towards slower-growing species, as suggested by Gould *et al.* (1993). This could mean that pioneer species such as *Eucalyptus grandis* grow and propagate relatively quickly, and have an advantage because they do not linger as seedlings for as long as native species such as *Milicia exelsea*. This may in turn explain why the native seedlings, in particular *M. exelsea*, had a higher mortality rate when exposed to termite attacks. Secondly, the sites in Lake Mburo National Park comprise heterogenous vegetation, and not the typical homogenous plantation sites where only a few species are represented. *Macrotermes* are fungus-growers, mainly feeding on leaf litter but also woody items that are not too big (Jouquet *et al*. 2011), such as seedlings. Attignon *et al.* (2005) found that this functional group was more abundant and more species-rich in plantations than in a semi-deciduous forest in Benin. The increased numbers of termites was explained by the dry soil conditions and the constant availability of leaf litter as a food source in the plantations (Attignon *et al*. 2005). Because plantation trees suffer from relatively high mortality rates, it is possible that fungus-growing termites feed on exotics based on food availability, and therefore also exist in large numbers in plantations. In other areas containing diverse vegetation, termites may feed based on preferences rather than food availability alone. This would explain why *Macrotermes* attack exotic seedlings in plantations, and prefer native seedlings in heterogenous areas, such as those found in Lake Mburo National Park. Finally, plantations typically support fewer ant species (Attignon *et al.* 2005), a common predator on *Macrotermes* in Africa (Bloesch 2008). Ant predation on termites in Lake Mburo National Park may reduce termite numbers, which in turn may influence termite predation on both exotic and native seedlings. Killing of termites by ants could also explain why *Macrotermes* mounds are often abandoned, which give plants the opportunity to settle on the otherwise impermeable and hard mound surface (Bloesch 2008). When recolonized, the termitaria already support vegetation that has grown too big for the *Macrotermes* to destroy it. In this sense, it is not termite preference alone controlling tree regeneration, but rather a combination of plant propagation and termite feeding strategies. It is possible that one or a combination of these processes are affecting termite abundance, feeding strategies or preferences, and therefore also effects of termites on seedling mortality in this study.

Inclusion of large herbivores increased mortality rates in all four species, which is supported by findings conducted throughout Africa (Moe *et al*. 2009b; O'Kane *et al*. 2012; Prins & van der Jeugd 1993). Large herbivores may also have positive impacts on seedling survival (Moe *et al*. 2014), but that was not the case in this study. There could be several reasons for this. Impact on mortality rates by large herbivores are highly dependent on ecosystem dynamics and the functional role the herbivores have in that ecosystem (Goheen *et al*. 2004). Furthermore, Goheen *et al*. (2004) showed that by allowing large herbivores to access seedlings, their survival was doubled compared to that of seedlings growing inside an enclosure in Kenya. Tree recruitment may therefore be enhanced by the presence of large herbivores, especially if these herbivores themselves are not the main predators on the seedlings. The main factors determining ungulate impact on seedling establishment are herbivore abundance and guild composition in a particular area (Moe *et al*. 2014). Thus, where browsing animals are found in large numbers relative to preferred food available, they can have profound effects on tree recruitment by intense and selective consumption of seedlings (Moe *et al*. 2014). It is clear from these results that herbivores in Lake Mburo National Park are directly influencing tree recruitment by browsing on seedlings. A similar study conducted in Botswana by Moe *et al*. (2009b) showed that woody seedling survival was reduced to only 32% in open plots, which coincides with the results in this study. In Lake Mburo National park, seedling survival in fenced plots varied between the exotic and native species, with mean values between 40-60% and 20-40%, respectively. Herbivore browsing was particularly important during the first period of measurements, the June-September dry season, when 40% of the *Eucalyptus grandis* and *Maesopsis eminii* seedlings died. High mortality rates during these ten weeks could be explained by drought stress or damage by baboons. At this stage, the seedlings were probably vulnerable to attacks by predators, although termites were less significant. Moe *et al*. (2009b) also noticed the rather large difference between mortality rates in open and fenced savannahs. In this study the results are slightly more variable, ranging from between 20-60% in differences between native and exotic mortality rates in open and fenced plots. This is probably due to the variable propagating strategies of the species included, and the impact of surrounding termites and other insects.

All 18 plots were surrounded by at least three active *Macrotermes* mounds within a radius of ten meters or less. Nevertheless, termites had little effect on growth rates when both exotic and native seedlings were unprotected. However, protection from termite attacks on seedlings had an additional small positive effect on seedling growth in all four species when combined with the exclusion of large herbivores. This suggests an additive role of termites in reducing tree regeneration. For instance, Buitenwerf *et al*. (2011) concluded that the role of Macrotermitinae species as consumers on leaf litter was impacted by the amount of rainfall and presence of herbivores in Benin. Interactions between large herbivores and termites in this study may explain why termites only had a marginal effect on seedling growth in the combination with large herbivores. Because large herbivores are attracted to termitaria and surrounding nutrient-rich vegetation, termites and herbivores are likely to interact, and possibly compete for the same food sources. Competition between termites and large ungulates may hence have influenced termite predation effects on seedling survival and growth (Sileshi *et al*. 2010). This would only occur where both prefer similar vegetation, such as tree seedlings. Although large herbivores were never observed *in situ* actually browsing on any of the seedlings, signs of herbivore activity on several of the plots were noticed. It should also be noted that the effects of termites may have been influenced by the presence of other insects. All nets were designed to specifically avoid termite disturbance and attacks on seedlings. However, without constant surveillance or local expertise when on site, it was difficult to separate one disturbance of termites from that of other soil-dwelling insects. Recently, Johnson & Riegler (2013) found that a soil-dwelling insect in Australia caused severe decrease in Eucalypt seedling growth rates. Eucalypts worldwide are subject to attacks by below-ground herbivores (Wylie & Speight 2011), and effects of termites in this experiment may not necessarily be caused by termites alone, but rather a combination of soil-dwelling insects including *Macrotermes*.

Exclusion of large herbivores increased seedling growth rates substantially compared to seedlings within open plots. This agrees with a more recent study conducted by Støen *et al*. (2013) in the same area, who found that plants in plots where herbivores had been excluded were taller and more abundant than in adjacent open plots. There was also a distinction made between the effects of large and medium-sized ungulates, where larger herbivores were found to facilitate tree regeneration, while smaller herbivores acted as predators on seedlings (Støen *et al*. 2013). Because herbivores in this study had a profound negative effect on seedling growth, it is likely that medium-sized herbivores, such as the impala *(Aepyceros melampus)*, dominated in seedling browsing over larger herbivores. In this sense, browsing by herbivores in Lake Mburo National Park should lead to reduced growth rates rather than facilitating seedling growth, which was the case in this study. This is also supported by findings stating the impala as an important browser in this area (Glosli 2008; Støen *et al*. 2013). Herbivores have been found to negatively affect seedling growth rates in several studies (Fornara & du Toit 2008; Levick & Rogers 2008; Sharam *et al*. 2006), and seedlings in this experiment showed significant differences in height between open and fenced plots. This was especially true for the exotic species *Eucalyptus grandis*, which according to Scogings *et al*. (2012) could be explained by its aggressive nature in combination with the oppression of native seedlings. Although Scogings *et al*. (2012) did not find any effects on seedling height in an exclusion experiment in South Africa, there was an immediate effect of herbivore exclusion on seedling height in this experiment, despite its relative short time span. This could be due to high browsing pressure of common herbivores in the park. Although illegal, Lake Mburo National Park also experiences livestock grazing (*pers. obs.)*, which may have affected seedling regeneration. It is common that sub-Saharan woodlands support high densities of domesticated mammalian herbivores (Gambiza *et al.* 2010), and cattle has been known to move across various areas within the park and its surrounding ecosystem (Rannestad *et al* 2006).

The role of termites in decreasing tree recruitment was seemingly dependent on herbivore activity in this study, but their role as pests in plantations and natural forests should not be underestimated. Uganda is subject to high rates of deforestation combined with rural poverty (Jacovelli 2009; Obua *et al*. 2010), which perhaps explains why forests are being replaced by plantations (FAO 2003). The growing demand for wood products in Uganda (Nyeko & Nakabonge 2008) requires information on seedling regeneration and seedling response to pests and growth constraints, such as termites and wild or domestic ungulates. A better understanding of the role of *Macrotermes* on native and exotic seedlings, and interactions between termites and large herbivores could provide valuable information in the management of local plantations and savannah ecosystem dynamics.

5. CONCLUSION

I conclude that browsing by large herbivores in Lake Mburo National Park negatively affect seedling survival and growth, thus changing woody tree regeneration. Termites have an additional small negative effect on seedling growth in Lake Mburo National Park, and decrease survival rates of native seedling species when combined with herbivore browsing. Also, termites are a more important cause of death for native than exotic seedlings in this study, while herbivores browse on all four species. Thus, I conclude that large herbivores reduce tree recruitment by acting as predators on exotic and native seedlings. Furthermore, I conclude that termites have an additional negative effect on tree regeneration by acting as predators on selected seedlings. I suggest that food availability as well as the functional role of termites and large herbivores as seedling predators influence their relative abundance and feeding preferences, and hence their effect on native and exotic seedling survival and growth.

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