



# Herbivores equalize the seedling height growth of three dominant tree species in an African tropical rain forest



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## ARTICLE INFO

### Article history:

Received 24 June 2013

Received in revised form 15 August 2013

Accepted 16 August 2013

Available online 30 September 2013

### Keywords:

Seedling herbivory

Korup–Cameroon

Light environment

*Microberlinia bisulcata*

Recruitment limitation

Herbivore exclusion

## ABSTRACT

Determining the impact of insect herbivores on forest tree seedlings and saplings is difficult without experimentation in the field. Moreover, this impact may be heterogeneous in time and space because of seasonal rainfall and canopy disturbances, or ‘gaps’, which can influence both insect abundance and plant performance. In this study we used fine netting to individually protect seedlings of *Microberlinia bisulcata*, *Tetraberlinia bifoliolata* and *Tetraberlinia korupensis* trees (Fabaceae = Leguminosae) from insects in 41 paired gap-understorey locations across 80 ha of primary rain forest (Korup, Cameroon).

For all species, growth in height and leaf numbers was negligible in the understorey, where *M. bisulcata* had the lowest survival after c. 2 years. In gaps, however, all species responded positively with pronounced above-ground growth across seasons. When exposed to herbivores their seedling height growth was similar, but in the absence of herbivores, *M. bisulcata* significantly outgrew both *Tetraberlinia* species and matched their leaf numbers. This result suggests that insect herbivores might play an important role in maintaining species coexistence by mitigating sapling abundance of the more palatable *M. bisulcata*, which in gaps was eaten the most severely. The higher ratio in static leaf damage of control-to-caged *M. bisulcata* seedlings in gaps than understorey locations was consistent with the Plant Vigour Hypothesis. This result, however, did not apply to either *Tetraberlinia* species. For *M. bisulcata* and *T. korupensis*, but not *T. bifoliolata* (the most shade-tolerant species), caging improved relative seedling survival in the understorey locations compared to gaps, providing restricted support for the Limiting Resource Model. Approximately 2.25 years after treatments were removed, the caged seedlings were taller and had more leaves than controls in all three species, and the effect remained strongest for *M. bisulcata*.

We conclude that in this community the impact of leaf herbivory on seedling growth in gaps is strong for the dominant *M. bisulcata*, which coupled to a very low shade-tolerance contributes to limiting its regeneration. However, because gaps are common to most forests, insect herbivores may be having impacts upon functionally similar tree species that are also characterized by low sapling recruitment much more widely than currently appreciated. An implication for the restoration and management of *M. bisulcata* populations in forests outside of Korup is that physical protection from herbivores of new seedlings where the canopy is opened by gaps, or by harvesting, should substantially increase its subcanopy regeneration, and thus, too, its opportunities for adult recruitment.

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## 1. Introduction

Most terrestrial plants are at some point in their lifetime susceptible to attacks from insects. Such attacks may slow the growth of individual plants, increase their mortality risks, hamper their reproduction, and possibly alter species abundance, distribution and composition in a community (Kulman, 1971; Coley and Barone, 1996; Carson and Root, 2000; Fine et al., 2004; Maron and Crone, 2006). Yet when plants are gradually eaten piece by piece,

as most appear to be, the negative impact on their fitness is more subtle than an overt death, as recurring bouts of even low levels of herbivory could accumulate and keep them small in size, weaken their competitive ability, and gradually shorten their longevity (Dirzo, 1984; Marquis, 2005). Such cryptic effects present a challenge for large, long-lived trees because new seedlings face large risks in attaining maturity in closed-canopy forests (Hartshorn, 1978; Canham, 1989; Connell, 1989; Nair, 2007).

Compounding this difficulty in understanding the impacts of chronic, non-fatal herbivory is that the kinds of damage from some insect herbivore guilds are more apparent than others. For example, attacks from leaf-gallers are obvious, and their galls can be counted; likewise, stem-borers leave noticeable signs of attack,

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and their pronounced effect on young tree growth and form can be great (e.g., Sullivan, 2003; Dalling et al., 2009). Yet the impacts of leaf chewers, which are a common guild of insects in tropical forests, are less clear and often mixed (Coley, 1983; Dirzo, 1984; Angulo-Sandoval and Aide, 2000; Howlett and Davidson, 2001; Pearson et al., 2003; Massey et al., 2006; Norghauer et al., 2008; Eichhorn et al., 2010). This uncertainty arises in part because of the following reasons: (1) Leaves can be eaten whole very quickly (especially when young) or they can be prematurely abscised, either outcome leading to 100% losses that may go undetected in observational studies (Coley, 1983; Cruz and Dirzo, 1987). (2) Leaf life spans varying both among and within tree species will influence the interpretation of static estimates of damage. And (3), external influences from neighbours, the abiotic environment, or tri-trophic interactions can modulate plant susceptibility to attacks (Coley and Barone, 1996; Dyer et al., 2010). Much more certain is that species identity is an important determinant of leaf herbivory of tropical tree seedlings and saplings (Cruz and Dirzo, 1987; Coley and Barone, 1996; Coley and Kursar, 1996; Gross et al., 2000; Pearson et al., 2003; Eichhorn et al., 2006; Massey et al., 2006).

Local resources that are in the least supply to plants may also influence the impact of herbivory by affecting an individual's ability to replace lost tissues and/or simply stay alive, as formulated by the Limiting Resource Model (LRM) of Wise and Abrahamson (2005, 2007). In a complementary way, greater availability of resources, especially of light, can promote vigorous growth in tree seedlings and may present more food (or food of better quality) for herbivores, expressed by the Plant Vigour Hypothesis (PVH) put forward by Price (1991). However, the net outcome of these non-mutually exclusive forces for individual seedling performance of co-occurring tree species is not well understood (Blundell and Peart, 2001; Norghauer et al., 2008; Salgado-Luarte and Gianoli, 2010). In forests, in the absence of canopy-replacing disturbances (e.g., fire, landslides, and hurricanes), light availability is only increased near the ground floor by stochastic, small-to-large openings in the canopy, mostly caused by tree and branch falls (Hartshorn, 1978; Denslow, 1987; Chazdon et al., 1996). In these 'gap' sites, plant morphological, physiological, and phenological acclimation to changing light intensities may alter interactions with herbivores and thus the net impact of them on plant fitness (Bazzaz and Pickett, 1980; Connell, 1989; Shure and Wilson, 1993; Chazdon, et al., 1996). Thus the PVH suggests that, in these canopy gaps, leaf damage caused by herbivores will be higher than in shaded understorey, although its impact on plant fitness should be lower because light is not as limiting a resource there as in the understorey, as predicted by the LRM.

To better assess the consequences of insect herbivory for tree regeneration and recruitment in the tropics, manipulations that directly quantify the impact of herbivory on very young trees are needed. To date, however, such manipulations in forests have mainly focused on excluding vertebrates (Sork, 1987; Howe, 1990; Osunkoya et al., 1993; Ickes et al., 2005)—or imposing one or more levels of stem- or leaf-damage (e.g., Dirzo, 1984; Jackson and Bach, 1999; Blundell and Peart, 2001; Sullivan, 2003; Norghauer et al., 2008). Very few studies have excluded insect herbivores *in situ*, particularly at spatial scales large enough to be (1) consistent with spatial patterns of gap dynamics in closed-canopy forests, (2) commensurate with tree species' statures and population sizes, and (3) covering species-specific dispersal shadows sufficiently. Using fine mesh netting, Pearson et al. (2003) protected three pioneer species in 12 artificial gaps in Panamanian secondary forest, as did Sagers and Coley (1995) for a tropical shrub in three large natural gaps, also in Panama. Fine et al. (2004) and Swamy and Terborgh (2010) similarly excluded insects but under mostly closed-canopy forest, in the Peruvian Amazon. Some studies have used insecticides to reduce herbivory

in forests (e.g., DeWalt et al., 2004), and in plantations (e.g., Plath et al., 2011), but their efficacy is debatable. Lastly, Dyer et al. (2010) manually removed insect herbivores from *Piper* shrubs, but such an approach is not feasible for large-scale forest experiments using many widely-spaced replicates. Apparently, no published study has physically excluded insects from one or more tree species in both disturbed (gap) and closed-canopy (understorey) habitats in a primary tropical rain forest to assess their impact on seedling growth and survival.

To this end, we carried out such an experiment in an African primary rain forest using three closely related canopy tree species: *Microberlinia bisulcata* A. Chev, *Tetraberlinia bifoliolata* (Harms) Haumann and *T. korupensis* Wieringa (Fabaceae = Leguminosae; subfamily Caesalpinioideae). Our specific hypotheses were: (1) The least shade-tolerant species, *M. bisulcata*, is eaten and has its growth in gaps impacted by insect herbivores to a greater extent than either *Tetraberlinia* species; (2) Leaves of all three species are damaged to a greater extent in gaps than the understorey (PVH); and (3) Protection from insect herbivores enhances seedling survival of all three species more in the understorey than gaps (LRM).

## 2. Materials and methods

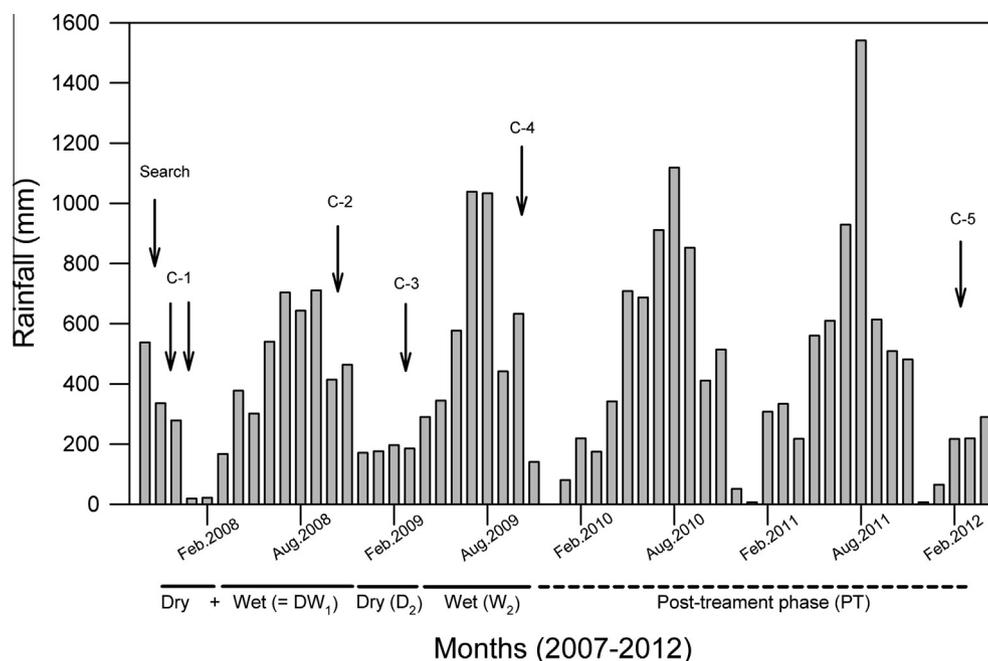
### 2.1. Study area and species

The experiment was done in moist lowland tropical forest in a 82.5-ha permanent 'P-plot' established in 1990–1991 (5°10'N, 8°52'E, see Newbery et al., 2013) in the southern part of Korup National Park (SW Cameroon). Mean ( $\pm$ SE) annual rainfall has been 5116  $\pm$  117 mm (1984–2011), almost entirely coming in the wet season between March and November (Fig. 1; see Newbery et al., 2006a). Soils in the P-plot are nutrient-poor in phosphorus and potassium compared to areas further north in the Park (Gartlan et al., 1986). These three study species form ectomycorrhizal associations that likely contribute to their canopy dominance: together they accounted for c. 60% of the large-tree basal area, and therefore play a major role in community and ecosystem processes (Newbery et al., 1988, 2013). Germinating seeds can yield three to six compound leaves on new seedlings of *M. bisulcata* but on *T. korupensis* and *T. bifoliolata* they form two opposite compound leaves. Those of *M. bisulcata* and *T. korupensis* consist of many small leaflets set along a rachis (i.e., they are microphyllous), but because those of *T. bifoliolata* have much larger leaflets (equivalent in size to typical mesophyllous leaves) theirs were considered as 'leaves'.

### 2.2. Experimental design

We used a split blocked design with new seedling cohorts that established from seed naturally dispersed in the 2007 wet season. Both *M. bisulcata* and *T. bifoliolata* mast-fruited that year while *T. korupensis* did not (Norghauer and Newbery, 2011). Nevertheless, a few large *T. korupensis* trees did reproduce and new seedlings were found in the western half of the P-plot. These seedlings can be assumed to be of similar age to those of *M. bisulcata* and *T. bifoliolata* (i.e., 2–5 months old by late November 2007).

The P-plot is 500 m (N–S) by 1650 m (E–W), and is divided into 330 marked subplots of 50-m  $\times$  50-m (0.25 ha each; see Appendix A, Fig. A.1). We searched 320 of them (80 ha total when excluding the westernmost column of subplots) between 28 November and 4 December 2007 for gaps containing new seedlings. Each gap was paired to an understorey location 30 m away from the gap edge on a random bearing, to form a 'block'. At both locations within each block, all suitable seedlings were flagged: these had to be firmly rooted in the ground, and not covered by neighbouring



**Fig. 1.** Time course of the field experiment that excluded insect herbivores (by caging) from newly established seedlings of three co-dominant tree species (*Microberlinia bisulcata*, *Tetraberlinia bifoliolata* and *T. korupensis*) in relation to the season rainfall pattern at Korup, Cameroon. Arrows indicate the median dates of the initial search for seedlings, treatment installation (=‘census 1’, C-1), and three subsequent censuses (C-2, C-3, and C-4) that corresponded to three experimental intervals: the latter part of the first dry season and most of the first wet season ( $DW_1$ ), the entire second dry season ( $D_2$ ), and nearly all of the second wet season ( $W_2$ ). Mesh cages and control tops were removed from all survivors at census 4 (C-4); the dashed line indicates the ‘post-treatment phase’ (PT) up to census 5 (C-5). February and August are generally the peak months of the dry and wet seasons.

vegetation in the seedling layer; and they needed to have at least the two new leaves in the cases of *T. bifoliolata* and *T. korupensis*, and at least four leaves in the case of *M. bisulcata*. A final consideration for suitability was that seedlings had to have mostly intact leaves, i.e., <5% of their leaf area missing. The understory areas were then searched for seedlings within a 10–20 m radius, or the areas were expanded until matching numbers of suitable seedlings were found. In this way, a total of 41 blocks were identified as being suitable for experimentation (Appendix A, Fig. A.1). In April 2009, for each block, the centres of seedling clusters in each canopy type (gap vs. understory) was estimated visually and marked with a plastic post. Across blocks, the mean ( $\pm$  SE) distance between centres of paired gap and understory locations was  $37.1 \pm 1.4$  m (median, 35.6 m; range, 15–65 m).

### 2.3. Installation of herbivory treatments

In each experimental block, we randomly assigned the flagged seedlings to grow with or without access by insect herbivores (‘caged’ vs. ‘control’). To reduce pressure from medium-sized leaf-chewing insects on individual seedlings, we built cages using Econet-B mesh (hole size of 1 mm  $\times$  4 mm; AB Ludwig Svensson, Sweden) that measured c. 40-cm  $\times$  40-cm in basal area and were 50-cm tall. Top flaps of cages were closed and kept taut, while controls had just 50-cm  $\times$  50-cm rooftops (sides open). (See Norghauer and Newbery, in press, for more details.) These herbivory treatments were installed over a 1-month period (13 December 2007–13 January 2008; see Fig. 1) and applied to 664 seedlings (Table 1). All treated seedlings had their initial heights measured perpendicular from the ground level to the tallest petiole-leaf junction, and their leaves counted and marked with thread. Each seedling was again evaluated for overall leaf damage just prior to the treatment installations. Since flagging in early December 2007, the majority (85%) of the 664 seedlings still had negligible leaf

damage (<5% leaf area missing), while 13.6% of them now had 5–20% damage (41 controls, 49 cages), and just nine seedlings (1.4%) had incurred moderate 20–50% damage (four controls, five cages). Between 18 December 2007 and the end of November 2009, litter fall on the tops of cages and on control roofs was removed every 5–7 days and transferred to the ground underneath.

### 2.4. Light measurements

We quantified light availability at individual seedling locations in two ways: (1) indirectly, using hemispherical digital photography, and (2) directly, by measuring instantaneous percentage of above-canopy light (PPFD: photon flux density of photosynthetically active radiation [400–700 nm] measured in units of  $\times 10 \mu\text{mol}/\text{m}^2/\text{s}$ ) transmitted through the canopy under overcast sky conditions (Messier and Puttonen, 1995). The latter are instantaneous measures of diffuse light known to be well correlated with the total daily mean %PPFD in other forests (Gendron et al., 1998). Details can be found in Appendix B.

To test whether mesh screening differentially obscured or limited light transmission to seedlings, we used the photon sensors to compare light levels inside the mesh treatments (caged vs. control) in the forest (Appendix C, Table C.1). In addition, *ex-situ* checks were made on new and worn mesh material to check their light transmission and any changes to them caused by weathering in the forest (Appendix D, Table D.1).

### 2.5. Growth and herbivory measurements in the treatment phase

After the start of the experiment (‘census 1’), seedlings were censused at three further times for changes in their size: on 9–14 November 2008 (‘census 2’), 11–15 March 2009 (‘census 3’), and 4–10 October 2009 (‘census 4’) (Fig. 1). Census dates were chosen to coincide best with changes between dry and wet seasons,

**Table 1**  
Mean ( $\pm$ SE) starting plant size of the three co-dominant tree species (Mb, *Microberlinia bisulcata*; Tb, *Tetraberlinia bifoliolata*; and Tk, *T. korupensis*) in the insect herbivore exclusion experiment in Korup National Park (Cameroon). Midway through the experiment, i.e. census 2, light availability was measured at all seedling locations: %PPFD<sub>mid</sub> is a direct measure of light under overcast conditions; %CO<sub>mid</sub> is canopy openness calculated from hemispherical photographs. For each variable, means not sharing the same small letters are significantly different at  $\alpha = 0.05$  in LMM analyses. Ranges are shown in parenthesis.

Plant sizes	Total no. seedlings	No. gaps or understorey locations	Gap		Understorey	
			Control	Caged	Control	Caged
<b>Height (cm)</b>						
Mb	388	34	21.0b $\pm$ 0.33 (13.5–30.3)	20.9b $\pm$ 0.35 (13.5–32.2)	20.1b $\pm$ 0.20 (16.0–26.5)	19.6b $\pm$ 0.21 (14.5–24.5)
Tb	172	18	19.6b $\pm$ 0.44 (13.7–25.6)	19.8b $\pm$ 0.40 (14.3–24.8)	21.2b $\pm$ 0.35 (17.1–27.3)	20.7b $\pm$ 0.27 (16.3–25.1)
Tk	104	10	23.5a $\pm$ 0.52 (19.4–29.0)	23.2a $\pm$ 0.58 (17.0–30.1)	20.9b $\pm$ 0.44 (14.7–25.5)	21.1b $\pm$ 0.40 (17.5–26.0)
<b>No. of leaves<sup>a</sup></b>						
Mb	388	34	5.9a $\pm$ 0.18 (4–12)	5.9a $\pm$ 0.16 (3–10)	4.4ab $\pm$ 0.07 (3–7)	4.5ab $\pm$ 0.06 (4–7)
Tb	172	18	4.2ab $\pm$ 0.12 (4–8)	4.1ab $\pm$ 0.08 (3–6)	4.0ab $\pm$ 0.00 (4–4)	4.0ab $\pm$ 0.00 (4–4)
Tk	104	10	4.1ab $\pm$ 0.34 (2–9)	4.1ab $\pm$ 0.37 (2–9)	2.0b $\pm$ 0.00 (2–2)	2.0b $\pm$ 0.00 (2–2)
<b>Light availability</b>						
%PPFD <sub>mid</sub> <sup>a</sup>						
Mb	388	34	5.36a $\pm$ 0.38 (0.81–22.2)	5.59a $\pm$ 0.35 (0.78–18.9)	0.59b $\pm$ 0.029 (0.17–1.88)	0.64b $\pm$ 0.04 (0.12–2.90)
Tb	172	18	5.39a $\pm$ 0.48 (1.62–15.5)	5.50a $\pm$ 0.49 (1.32–13.7)	0.73b $\pm$ 0.07 (0.47–0.59)	0.77b $\pm$ 0.08 (0.54–0.63)
Tk	104	10	6.04a $\pm$ 0.91 (1.64–19.3)	4.11a $\pm$ 0.34 (1.07–9.54)	1.10b $\pm$ 0.37 (0.06–7.94)	1.03b $\pm$ 0.30 (0.33–6.49)
%CO <sub>mid</sub>						
Mb	388	34	7.69a $\pm$ 0.17 (4.44–11.7)	7.86a $\pm$ 0.19 (2.91–12.9)	5.53b $\pm$ 0.11 (2.95–7.96)	5.48b $\pm$ 0.01 (2.77–8.05)
Tb	172	18	8.23a $\pm$ 0.26 (5.32–10.9)	8.46a $\pm$ 0.33 (4.86–14.1)	5.48b $\pm$ 0.18 (3.31–9.27)	5.96b $\pm$ 0.17 (1.13–8.62)
Tk	104	10	9.21a $\pm$ 0.33 (6.43–14.3)	8.68a $\pm$ 0.35 (4.38–13.1)	5.64b $\pm$ 0.22 (4.52–9.06)	5.79b $\pm$ 0.18 (4.28–8.29)

<sup>a</sup> Log-transformed in LMMs.

which resulted in three successive census intervals for studying the growth and herbivory of seedlings: DW<sub>1</sub>, D<sub>2</sub>, and W<sub>2</sub> (see Fig. 1). At each census we measured the relaxed seedling height and counted total number of leaves, using colour-coded copper wire to distinguish between those produced since the last census (new) and those present before (old). Individual leaf damage on all new leaves produced in gaps, and on all leaves present at understorey locations, were scored visually according to five damage classes: <5%, 5–20%, 20–50%, 50–75%, >75% of leaf area missing. Similarly-scaled indices have been used in other field studies to rapidly and reliably gauge standing levels of leaf herbivory in a non-destructive way (Garcia-Guzman and Dirzo, 2001). At censuses 2 and 4, in gaps alone, we recorded the proportion of leaves that showed clear evidence of insect leaf chewing; and for the sample at census 4 all insect-chewed leaves present were grouped into either <50% or  $\geq$ 50% damage classes. To estimate maximum leaf areas, up to five of the largest intact leaves on gap seedlings were measured for their lengths and widths during census 4 (end of W<sub>2</sub>). Then, at all seedling locations (dead or alive), the heterospecific vegetation was quantified in a systematic way by one of us (Appendix E). Further details on height measurements, leaf area estimations and the enlargements of cages can be found in Appendix F.

## 2.6. Long-term impacts of herbivory

Soon after census 4, all mesh cages and control tops were removed (27 October–4 November 2009), and all seedlings alive in gaps received each a numbered aluminum tag. To gauge the longer-term effects of herbivores on post-establishment tree growth, the gaps were revisited and searched for surviving seedlings on 3–4 March 2012 (hereafter ‘census 5’, Fig. 1), c. 27 months later (2.3 years), which represented a ‘post-treatment’ phase (‘PT’ interval in Fig. 1). By this time many gaps were expected to have closed up. The survivors from the starting sample were measured for stem height and their leaves counted.

## 2.7. Data analysis

We used a linear mixed model (LMM) approach with REML estimation in GenStat v.14.1 (Payne et al., 2009). The random factor

was the experimental block. The fixed factors were canopy type within each block (gap vs. understorey), and nested within each canopy type, species present crossed with the randomized herbivore treatments (caged vs. control) and their interactions. Hence this was a 2  $\times$  3  $\times$  2 partly-nested factorial block design: the statistical unit of replication for testing the main effect of canopy type was location, whereas for all other tests of main and crossed effects it was the individual seedling (see Quinn and Keough, 2002; Galwey, 2006 for design aspects). Based on earlier work onsite (Green and Newbery, 2001a,b), we anticipated a three-way interaction between the fixed factors, and were therefore primarily interested in contrasts among the 12 treatment means. We carried out sequential multiple pairwise comparisons of means adjusted for block effects, which controlled for the family-wide Type 1 error rate even in those cases where the omnibus test for the three-way interaction was not significant (Day and Quinn, 1989; Hancock and Klockers, 1996; see Appendix G for more details). All arithmetic means presented in the tables and figures are based on the raw data (i.e., not transformed or back-transformed).

### 2.7.1. Growth rates

To standardize for differences in initial plant height, we used relative growth rate, calculated as:  $RGR-HT = [\ln(ht_2) - \ln(ht_1)] / [t_2 - t_1]$ ; where  $ht_1$  and  $ht_2$  are heights at times  $t_1$  and  $t_2$  corresponding to the start and end of the time interval between censuses (units of  $\text{cm cm}^{-1} \text{ year}^{-1}$ ). The lengths of the three time intervals DW<sub>1</sub>, D<sub>2</sub> and W<sub>2</sub> were 0.875, 0.333 and 0.666 years respectively; and hence the whole treatment interval (DW<sub>1</sub> + D<sub>2</sub> + W<sub>2</sub>; Fig. 1) was 1.875 years. Likewise, the net change in total numbers of leaves ( $nl$ ) on seedlings was also calculated as a relative growth rate ( $RGR-LV, nl nl^{-1} \text{ year}^{-1}$ ). One LMM was fitted separately for  $RGR-HT$  and  $RGR-LV$  in each of these intervals. Given in Appendix G are further details on the analyses, which outliers were removed, and how long-term effects were modeled after accounting for light availability and levels of leaf harvesting.

It is possible that  $RGR$ , as formulated above, can be biased by starting plant sizes (i.e.,  $ht_1$ ), especially when the sample consists of different-aged seedling cohorts, or of annual plant species that change rapidly in biomass, or when compared across different-sized life-forms. However, this issue did not apply to our particular

dataset because the caged vs. control samples of each species had virtually identical starting height distributions and were similar-aged, and any differences in heights among species were very small in absolute terms (see SEs and ranges in Table 1).

### 2.7.2. Leaf damage

Following Garcia-Guzman and Dirzo (2001), individual leaf scores (1–5) were first averaged for each seedling to not miss the contribution of infrequent cases of severe herbivory (Cruz and Dirzo 1987). Three sets of static damage indices—one each for DW<sub>1</sub>, D<sub>2</sub>, and W<sub>2</sub> leaves—for gap data only were analyzed using non-parametric tests. Rates of damage to these new gap leaves were approximated by first converting seedlings' mean scores to their percentage equivalents and dividing by months in a given time interval(s), then averaged across the treatment period. This was done for the understorey too, for comparative purposes, but instead using accumulated months throughout the period (because mostly the same set of leaves were scored through successive time intervals).

For new leaves clearly damaged by insects in gaps, three further indices using proportions were developed (there was very little leaf production at understorey locations). These indices were (1) the proportion of new leaves in DW<sub>1</sub> chewed by insects; and (2) the proportions of all leaves present at the end of the treatment phase chewed by insects; and of the latter, (3 and 4) those with <50% or ≥50% damage respectively. For indices (1) and (2), a general linearized mixed model (GLMM) was used, with a binomial error distribution and logit link, for which the binomial totals were the number of new leaves (1) and total leaves (2) and the response variable the number of damaged leaves. For indices (3) and (4), the means of proportions were compared using 95% confidence intervals because the mixed models fitted poorly to the data.

### 2.7.3. Evidence for PVH and LRM

Unlike for rates of leaf damage, comparing static damage levels on control seedlings in gaps vs. the understorey was not feasible because in the latter environment damage accumulated over time, while in the former one only those leaves newly-produced in each interval (DW<sub>1</sub>, D<sub>2</sub>, and W<sub>2</sub>) were scored. Following from the Plant Vigour Hypothesis (PVH), we expected the ratio of damage levels for control/caged treatments to be higher within gaps than within understorey. To test this PVH, we averaged seedling-level leaf damage from DW<sub>1</sub>—as this provided the largest sample sizes for each species—over each gap and understorey location, and used a standard (one-tailed) *t*-test since the distribution of ratios for each species were not skewed.

Similarly, because above-ground growth was negligible in the understorey, we could not test predictions of the Limiting Resource Model (LRM) using heights or leaf numbers. For many rain forest species though, persistence of their seedlings in the understorey until light conditions improve is vital for recruitment (Canham, 1989; Kitajima, 1994). We therefore tested the specific prediction that the benefit of caging relative to controls would be negligible for overall survival in gaps (where light is not a limiting resource), whereas this difference in survival would be positive at understorey locations (i.e., caged – control > 0). For each species, we first removed all cases of stems clipped near their bases by small mammals (presumably rodents). Then, separately for each canopy type, we calculated the 95% confidence intervals for the difference in treatment survival proportions (following Agresti, 2007). If the 95% confidence limits (CL) did not overlap with zero or have negative values, we could conclude that there was a significant difference between the treatments in the hypothesized direction.

## 3. Results

### 3.1. Forest light environments

Seedlings located in gaps received 5–9 times more light than those in the understorey locations when directly measured as %PPFD transmission midway through the experiment (Table 1; Appendix H, Table H.1; Appendix I, Fig. I.1). Light availability was also significantly greater in gaps when measured indirectly, using either percent canopy openness (%CO<sub>mid</sub>, Table 1) or the total PPFD calculated from the hemispherical photographs (PPFD means ± SE: 6.16 ± 0.09 vs. 3.29 ± 0.04 mol m<sup>-2</sup> d<sup>-1</sup>; Appendix H). No significant differences were detected between herbivory treatments in either light environment.

Two years after the experiment started, more light still reached seedlings in gaps than in the understorey (total PPFD: 4.53 ± 0.07 vs. 4.06 ± 0.04 mol m<sup>-2</sup> d<sup>-1</sup>; Appendix H, Table H.1). However, because gaps grew in from below and above, their %CO<sub>end</sub> was reduced to 6.68 ± 0.07%. Conversely, because new gaps naturally formed in the forest over the two-year period, %CO<sub>end</sub> increased slightly to 7.12 ± 0.08% in the understorey (Appendix J, Fig. J.1). (A given level of %CO can transmit differing amounts of PPFD depending on the orientation of the sky pixels in hemispherical photographs.) As before too, no significant differences were detected between or among treatment combinations (Appendix H). Moreover, at all live and dead seedling locations in gaps (*n* = 338), the %PPFD<sub>end</sub> was very similar between caged and control treatments for all three species (Appendix H).

In gaps, the caged and control treatments had similar levels of heterospecific vegetation cover, which (not surprisingly) was greater than at the understorey locations. In the latter, cages had significantly less cover than the controls (Appendix E, Fig. E.1), but this was only a 4% absolute difference due to more patchy cover around the two *Tetraberlinia* species.

### 3.1. Growth of tree seedlings

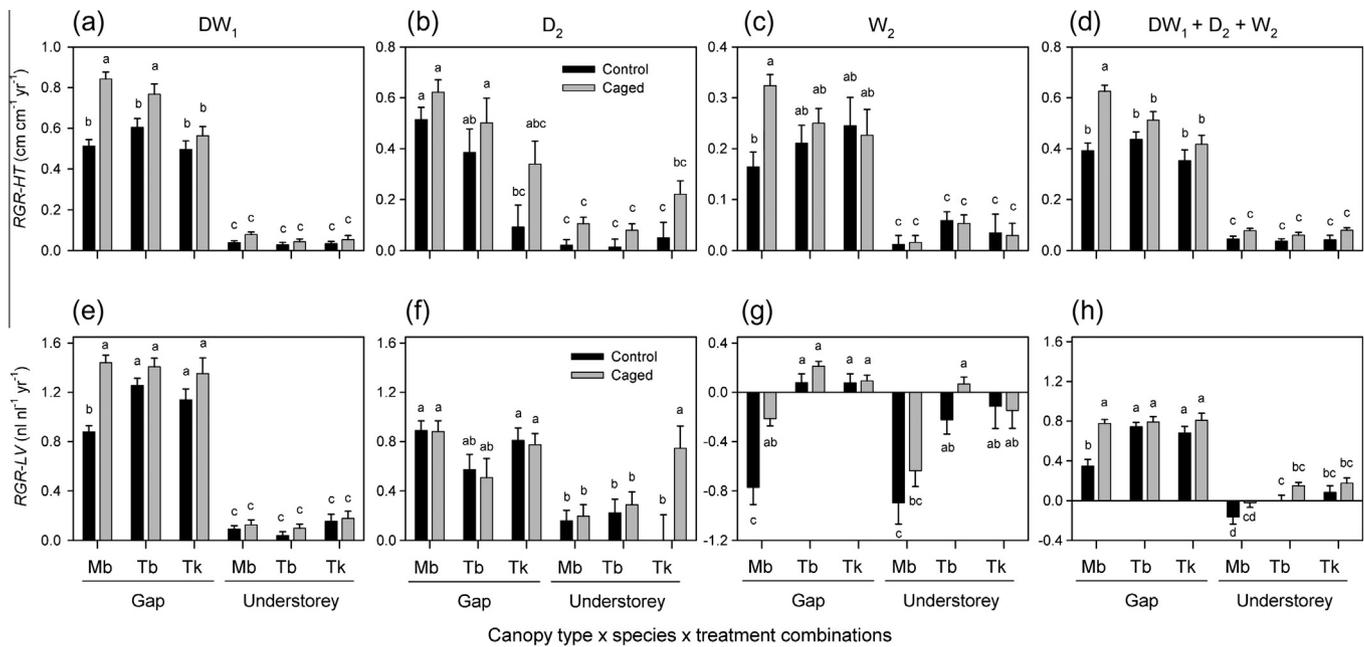
#### 3.1.1. Height growth

Relative growth rates in height (RGR-HT) of all three species were higher in gaps than at understorey locations where they instead stayed small (Fig. 2a and d; Appendix H, Table H.2.). In the DW<sub>1</sub> interval, seedlings in gaps not only grew much faster, but their growth was significantly greater for both *M. bisulcata* and *T. bifoliolata* (not for *T. korupensis*) in cages than controls. From census 1 to 4 (including now a second dry season and another wet season), all species showed diminished growth rates in gaps, yet the ranking of *M. bisulcata* > *T. bifoliolata* > *T. korupensis* when caged was still maintained such that now *M. bisulcata* significantly grew faster than either *Tetraberlinia* species (Fig. 2d). No significant benefit of herbivore exclusion was detected for the latter two species.

For D<sub>2</sub> there appeared to be little species-specific growth advantage gained by caging vs. control for either canopy type (Fig. 2b; Appendix H, Table H.2.), though the difference in growth rates was still significant between treatments averaged over canopy types and species. When averaged over treatments, growth rates were significantly greater in gaps than at understorey locations for *M. bisulcata* and *T. bifoliolata*, yet insignificantly so for *T. korupensis*. During the next interval, W<sub>2</sub>, height growth rate closely mirrored the pattern seen in DW<sub>1</sub>, in that caged *M. bisulcata* seedlings in gaps grew at nearly twice the rate of their conspecific controls (Fig. 2c) whereas both *Tetraberlinia* species lacked such a pronounced difference.

#### 3.1.2. Leaf dynamics

Relative growth rates in terms of leaf number (RGR-LV) showed similar patterns to those in terms of height in the DW<sub>1</sub> interval.



**Fig. 2.** Relative growth rates in height,  $RGR-HT$  (a–d), and leaf numbers  $RGR-LV$  (e–h), of *Microberlinia bisulcata* (Mb), *Tetraberlinia bifoliolata* (Tb) and *T. korupensis* (Tk) tree seedlings (means  $\pm$  SE) for two insect herbivore treatments (caged vs. control) under two canopy types (gap vs. understorey) at Korup, in (a, e) the first dry and wet season ('DW<sub>1</sub>'), in (b and f) the next dry season ('D<sub>2</sub>'), and (c, g) in the next wet season ('W<sub>2</sub>'); and (d, h) over the entire experimental period since census 1 ('DW<sub>1</sub> + D<sub>2</sub> + W<sub>2</sub>'). Dates of censuses and intervals are given in Fig. 1; sample sizes (range 13–96) are given in Appendix M. Means not sharing the same small letters within any one panel are significantly different at  $P \leq 0.05$ . Note the different scales of the panel y-axes.

However, in gaps, while *Microberlinia* lagged behind the two *Tetraberlinia* species in maintaining its leaf numbers, when protected from insect herbivores, all three species had similar growth in leaf numbers (Fig. 2e; Appendix H, Table H.2). By the end of the treatment phase (census 4), *M. bisulcata* seedlings caged in gaps had grown twice as fast as under controls, but had a marked negative growth rate in the understorey, implying a net loss in leaf numbers (Fig. 2h).

While the growth rate in D<sub>2</sub> did not differ significantly for caged and control seedlings averaged over canopy type and species, our conservative pairwise comparisons did indicate a significant difference for *T. korupensis* growth in the understorey (Fig. 2f; Appendix H, Table H.2.). Averaged over treatments, *M. bisulcata* grew slightly faster than *T. korupensis* in gaps, and was c. 60% faster than *T. bifoliolata*. In W<sub>2</sub>, the comparisons further suggested that *M. bisulcata* benefited the most from caging, and significantly so in gaps (Fig. 2g). In the understorey, however, all three species' controls experienced net losses in their leaf numbers (Fig. 2g).

Few, or almost no, leaves were produced in the understorey for any of the species, but in gaps there were many more, especially when cages were compared with controls for *M. bisulcata* (see Appendix K, Fig. K.1). The low leaf numbers in the understorey (Fig. 2e–h) therefore reflected a lack of growth rather than high rates of turnover.

In gaps, light availability had a generally positive and highly significant effect on a leaf maximal area (LMM on log-transformed mean values: covariate term, %PPFD<sub>mid</sub>,  $F_{1, 248.4} = 55.69$ ,  $P < 0.001$ ). Caged *M. bisulcata* seedlings were able to produce leaves that were on average 60% larger than their conspecific controls (Table 2), whereas the *Tetraberlinia* species both had leaves of similar size under the two treatments (species  $\times$  treatment term,  $F_{2, 214.8} = 8.68$ ,  $P < 0.001$ ).

### 3.2. Leaf damage

In both gaps and understorey, caging reduced the mean rate of missing leaf area on seedlings significantly for *M. bisulcata* and *T. bifoliolata*, but not *T. korupensis* (Fig. 3). In the DW<sub>1</sub> interval, the sig-

nificant differences in median static damage scores between treatments (caged vs. control) on new leaves in gaps were greatest for *M. bisulcata* seedlings, but 50% lower for *T. bifoliolata* and *T. korupensis* (Table 3). In the D<sub>2</sub> and W<sub>2</sub> intervals, gap controls had less static damage than conspecific caged seedlings except for *T. korupensis* in the second wet season (W<sub>2</sub>; Table 3). Among species in gaps, the control seedlings of *M. bisulcata* had significantly more such damage than those of *T. bifoliolata* in each of the three time intervals (Mann–Whitney tests, range of  $U$ -values: 263–431,  $P$ -values  $< 0.001$ – $0.002$ ,  $n = 59$ – $79$ ); though also greater than *T. korupensis*, this difference was not significant in D<sub>2</sub> or W<sub>2</sub> ( $U$ -values: 616 and 227,  $P = 0.173$ ,  $0.432$ ,  $n = 89$ ,  $48$ , respectively; Table 3) unless damage was expressed instead as rates of leaf area lost (see Fig. 3).

Scoring of explicitly insect-chewed leaves in gaps only confirmed that cages incurred significantly fewer signs of insect attack there than controls, as expected if the treatment had worked. However, *T. bifoliolata* had significantly 18.2% and 23.6% fewer leaves damaged in this way than *M. bisulcata* or *T. korupensis*, respectively, in the DW<sub>1</sub> interval (see Appendix L, Fig. L.1a). When all leaves present at the end of the whole treatment phase (census 4) were assessed, *M. bisulcata* had slightly fewer insect-damaged leaves on its control seedlings than *T. korupensis* (Appendix L, Fig. L.1b). However, when the severity of leaf damage was taken into account, *M. bisulcata* had 2–3 times more leaves than *T. bifoliolata* and *T. korupensis* with heavy ( $\geq 50\%$ ) damage, and correspondingly fewer with lighter ( $< 50\%$ ) damage (Fig. 4).

More damage on control than caged leaves in gaps as compared to the understorey is one testable prediction of the Plant Vigour Hypothesis (PVH). Here, the ratios between control and caged levels of static damage were significantly different between canopy types for *M. bisulcata* ( $t = 2.93$ , d.f. = 56) and thus consistent with the PVH. However, results were not consistent with the PVH for *T. bifoliolata* ( $t = 0.28$ , d.f. = 31) or *T. korupensis* ( $t = -0.49$ , d.f. = 14; see Fig. 5). Further support for the PVH as it applies to *M. bisulcata* can be seen in the significantly higher rates of leaf damage on controls in gaps than in the understorey; this result was also found for *T. bifoliolata*, but not *T. korupensis* (see Fig. 3).

**Table 2**

Light levels and leaf size of the seedlings of three tree species (Mb, *Microberlinia bisulcata*; Tb, *Tetraberlinia bifoliolata*; and Tk, *T. korupensis*) growing in canopy gaps at census 4—the end of the experimental treatment period (see Fig. 1)—that were protected (caged) and unprotected (control) from insect herbivores at Korup National Park (Cameroon). Also given are the final absolute sizes for survivors at census 5, that is, after a 'post-treatment' period of c. 2.25 years (see Fig. 1). %PPFD<sub>end</sub> is a direct measure of light under overcast conditions; %CO<sub>end</sub> is canopy openness calculated from hemispherical photographs. Means (±SE); ranges are shown in parenthesis.

	n <sup>a</sup>	Mb		n <sup>a</sup>	Tb		n <sup>a</sup>	Tk	
		Control	Caged		Control	Caged		Control	Caged
Light availability <sup>d</sup>									
%PPFD <sub>end</sub> <sup>b</sup>	47,93	3.27 ± 0.56 (0.34–21.13)	3.57 ± 0.19 (0.19–16.87)	37,41	3.87 ± 0.56 (0.56–14.59)	3.89 ± 0.51 (2.42–11.97)	21,27	4.53 ± 0.87 (0.51–17.04)	3.58 ± 0.63 (0.34–11.03)
%CO <sub>end</sub> <sup>c</sup>	47,94	6.69 ± 0.19 (4.27–10.84)	6.80 ± 0.13 (3.94–10.70)	38,41	6.67 ± 0.18 (3.73–8.59)	6.78 ± 0.22 (3.19–9.36)	21,26	6.75 ± 0.21 (4.44–8.48)	6.29 ± 0.19 (4.17–8.87)
Leaf size									
Max. area per leaf (cm <sup>2</sup> )	47,60	24.7 ± 1.6 (8.67–64.2)	39.4 ± 1.6 (10.1–93.2)	36,39	24.1 ± 1.9 (8.96–58.6)	27.0 ± 1.7 (8.51–50.6)	21,24	39.0 ± 2.9 (22.0–74.0)	44.6 ± 3.8 (9.40–102.4)
Post-treatment sizes									
Height (cm) <sup>b</sup>	25,60	63.5 ± 8.8 (15.0–241.0)	100.9 ± 8.9 (38.5–339.0)	30,30	61.3 ± 6.4 (21.0–182.5)	73.5 ± 8.6 (29.5–223.0)	13,22	56.1 ± 8.0 (18.0–122.5)	60.8 ± 4.4 (18.5–101.0)
No. Leaves <sup>b</sup>	25,60	17.8 ± 4.3 (3–109)	40.4 ± 7.9 (5–263)	30,30	14.0 ± 2.0 (2–58)	20.0 ± 2.8 (2–70)	13,22	8.8 ± 2.0 (2–26)	12.1 ± 1.8 (2–42)

<sup>a</sup> The sample counts are given as 'control, caged' treatments.

<sup>b</sup> Log-transformed in LMMs.

<sup>c</sup> One outlier had to be removed to fit LMM.

<sup>d</sup> Sample means shown are for survivors only.

### 3.3. Correlations between leaf damage and seedling growth

On a per-species basis, *RGR-HT* was not significantly correlated with static damage to new leaves of any of the tree species in the DW<sub>1</sub> interval (*P*-values: 0.183 to 0.433). In D<sub>2</sub>, though, it was significantly negatively correlated for *M. bisulcata* (Spearman's coefficient,  $r_s = -0.311$ ,  $P = 0.012$ , d.f. = 63), but not for *T. bifoliolata* ( $r_s = 0.027$ ,  $P = 0.917$ , d.f. = 36), and positively for *T. korupensis* ( $r_s = 0.441$ ,  $P = 0.014$ , d.f. = 22). In W<sub>2</sub>, no significant correlations were found (*P*-values: 0.066, 0.157 and 0.104, respectively).

Between-period correlations yielded a significant negative correlation between damage in DW<sub>1</sub> and growth in D<sub>2</sub> for *M. bisulcata* ( $r_s = -0.262$ ,  $P = 0.012$ , d.f. = 89), but a positive one for *T. korupensis* ( $r_s = 0.459$ ,  $P = 0.005$ , d.f. = 24), for which growth in W<sub>2</sub> and damage in D<sub>2</sub> was also positively correlated ( $r_s = 0.385$ ,  $P = 0.019$ , d.f. = 20). The remaining three correlations were not significant (*P*-values: 0.312–0.889).

### 3.4. Survival of non-stem-clipped seedlings

The proportions of seedlings that survived in control/caged treatments in the understorey were 0.302/0.452, 0.565/0.826, and 0.786/0.791 for *M. bisulcata*, *T. korupensis*, and *T. bifoliolata* respectively; and likewise for gaps the proportions were 0.854/0.940, 0.913/0.931 and 0.927/0.953. The ranking of survivorship-values was accordingly *T. bifoliolata* > *T. korupensis* > *M. bisulcata*, under both canopy types.

The Limiting Resource Model (LRM) suggests that the mortality risk of controls would exceed that of caged seedlings in the understorey, but not in the gaps where light is less limiting. Consistent with this prediction, caging improved the survivorship of *M. bisulcata* and *T. korupensis* more at the understorey locations than in gaps (Fig. 6). The 95% confidence intervals for the difference between caged and control proportions of seedlings surviving in the understorey were clearly positive for *M. bisulcata* (confidence limits, CLs: 0.129, 0.286), yet only just positive for *T. korupensis* (CLs: 0.006, 0.516). In the gaps, the intervals for treatment differences contained negative values for each of these two species (CLs respectively,  $-0.089$ , 0.260 and  $-0.129$ , 0.165). By contrast, there was no benefit of caging on *T. bifoliolata* survivorship in the

understorey (CLs:  $-0.169$ , 0.179; in gaps, CLs:  $-0.074$ , 0.128 at understorey locations; Fig. 6).

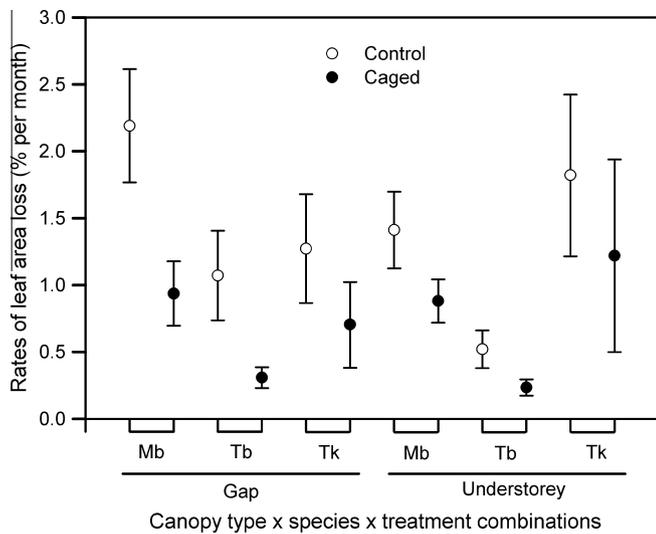
### 3.5. Long-term effects of herbivory

Final stem height at census 5 was significantly greater in caged than control seedlings when averaged over all three species, with no significant interaction detected (log-transformed response, treatment term,  $F_{1, 151.9} = 10.39$ ,  $P = 0.002$ ; species × treatment term,  $P = 0.322$ ; Table 2). Averaged over treatments, seedlings of *M. bisulcata* were taller than those of either *Tetraberlinia* species (species term,  $F_{2, 141.7} = 10.39$ ,  $P < 0.001$ ). Similar results were obtained for total numbers of leaves on survivors (log-transformed response, all four main model terms, *P*-values < 0.001; interaction term,  $P = 0.836$ ; one outlying value for *T. bifoliolata*), except that now *M. bisulcata* and *T. bifoliolata* were similar to one another in having significantly more leaves than *T. korupensis* (Table 2).

## 4. Discussion

### 4.1. Herbivory in the tropics

A better understanding of plant-insect herbivore interactions in early post-dispersal tree dynamics in tropical forests may come from field experiments that achieve two aims together, as done here. The first is to directly reduce, through physical exclusion, the herbivore pressure on new seedlings to assess their impact on growth and survival, and the second, to protect seedlings growing along a light resource gradient (i.e., one that includes both understorey and gap environments). In this part of Korup the soils are sandy and especially lacking in phosphorus and potassium, and so impacts of leaf herbivory should take on greater importance in terms of fitness of the affected plants (Coley et al., 1985; Fine et al., 2004). Among four tropical forest communities, Coley and Kursar (1996) recorded the lowest rates of herbivory on leaves from saplings at Korup. It is thus intriguing from both ecological and evolutionary perspectives to find in such a resource-poor environment that the most dominant canopy species in the forest community, *M. bisulcata*, is also a highly palatable one. Orthoptera nymphs were repeatedly seen eating leaves of all three tree species; as occasionally were leaf-cutting bees on *M. bisulcata* and *T.*



**Fig. 3.** Overall rates of leaf damage, expressed as loss in leaf area, calculated for *Microberlinia bisulcata* (Mb), *Tetraberlinia bifoliolata* (Tb) and *T. korupensis* (Tk) tree seedlings for two insect herbivore treatments (caged vs. control) under two canopy types (gap vs. understorey) at Korup. These were conservative estimates (i.e., underestimates) for missing leaf area in gaps because not all leaves had flushed at the start of each time interval(s). Symbols are means with their 95% confidence limits as bars. Sample sizes (range 20–97 seedlings) are given in Appendix M.

*korupensis* leaflets. A stick insect (Phasmida) was found eating *M. bisulcata*. Lepidopteran pupae were found on *M. bisulcata* (in gaps), from which a c. 1.5-cm-long unidentified moth (with a fluorescent-yellow body) was reared. An unknown black and orange caterpillar was photographed defoliating mature *T. bifoliolata* leaves.

#### 4.2. Herbivory and growth in gaps

Under natural conditions (i.e. controls) these species appear equally competitive in terms of height growth. This result on its own does not support the notion that these tree species can differentially partition the light environments of gaps, or that there is a height growth advantage trade-off with survival in the low-lit understorey (Dalling and Burslem, 2005; Kitajima and Poorter, 2008). However, reducing herbivore pressure using cages revealed that *M. bisulcata* could outgrow the other two species under gap conditions. A causal role for insect herbivores diminishing the growth rates of *M. bisulcata*, while having a much lesser impact

on the *Tetraberlinia* species, is further supported by the former's much higher levels of leaf damage in gaps, especially in terms of numbers of leaves severely eaten. There exists, then, the possibility that light resources in the forest, at the broader gap-understorey scale, are being partitioned by *M. bisulcata* and *Tetraberlinia* seedlings in the form of such a trade-off. But such a mechanism of niche differentiation is one that is clearly being mitigated by insect herbivores.

That *M. bisulcata* has the best height growth potential and is the most light-responsive among the dominant species agrees with results of an earlier nursery experiment under herbivore-free conditions (Green and Newbery, 2001a). However, in a matching field trial at Korup both *Tetraberlinia* species gained more biomass than did *M. bisulcata* as light levels increased in the forest (Green and Newbery, 2001b). Our new results confirm the suggestion put forward by these earlier studies, and do explain the discrepancy; namely that insect herbivores caused heavy leaf losses on *M. bisulcata* when its seedlings were better lit in gaps.

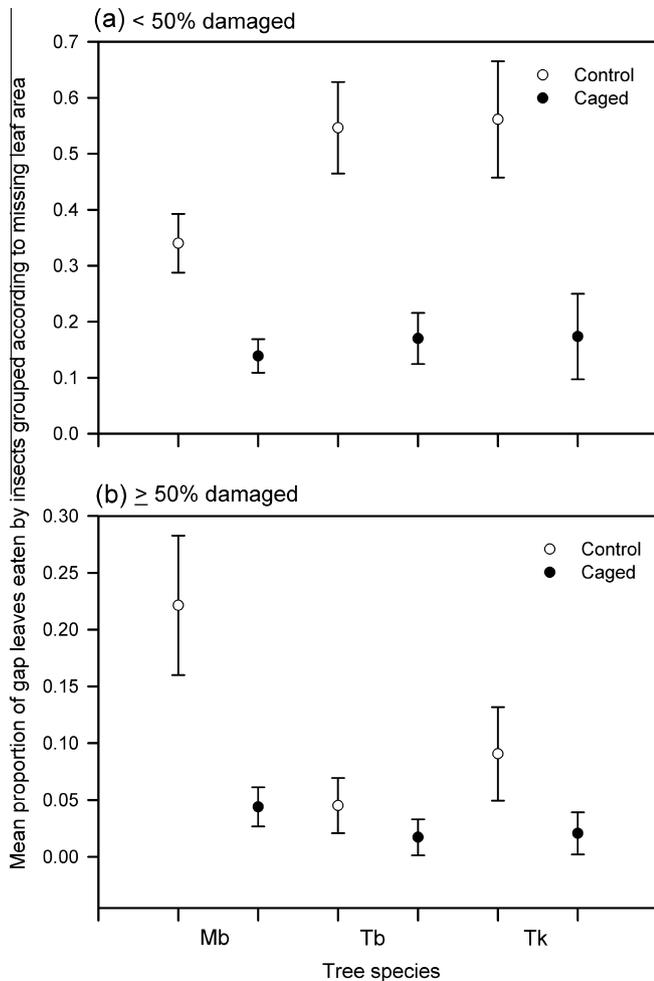
Nevertheless, leaf damage was quite variable within and among species across seasons. When converted to percentage leaf area missing, maximum losses on control seedlings in gaps during the DW<sub>1</sub> period were 80% on *M. bisulcata* and 29% and 28% for *T. bifoliolata* and *T. korupensis*, respectively. That these values increased for leaves produced in the second wet season (W<sub>2</sub>) for the two latter species (60% and 47%; cf. 89% for *M. bisulcata*) suggests that there was a general increase in herbivore pressure, possibly due to increased rainfall. Although our scoring missed cases of complete leaf loss and premature leaf abscission (Coley, 1983; Cruz and Dirzo, 1987), such cryptic events were part of the overall impact of insect herbivores on plant growth in gaps since controls were being compared with caged seedlings. Our empirical study joins the very few (Sagers and Coley, 1995; Fine et al., 2004) to have experimentally shown that leaf-chewing insects, in contrast to stem shoot-borers (e.g., Sullivan, 2003; Nair, 2007; Dalling et al., 2009), do have an impact on tropical seedling growth under natural forest conditions.

The caged-to-control ratios of mean scores for static leaf damage (−1.0) and of the proportion of leaves chewed for the three species in gaps in the first growing year were 3.0–6.2, in line with results from other tropical forest studies (Sagers and Coley, 1995; Pearson et al., 2003; Boege, 2004). At the canopy scale, the ratio in leaf damage was higher in gaps than at understorey locations for *M. bisulcata*, as were the damage rates of controls, which is consistent with the Plant Vigour Hypothesis (PVH, Price, 1991). A

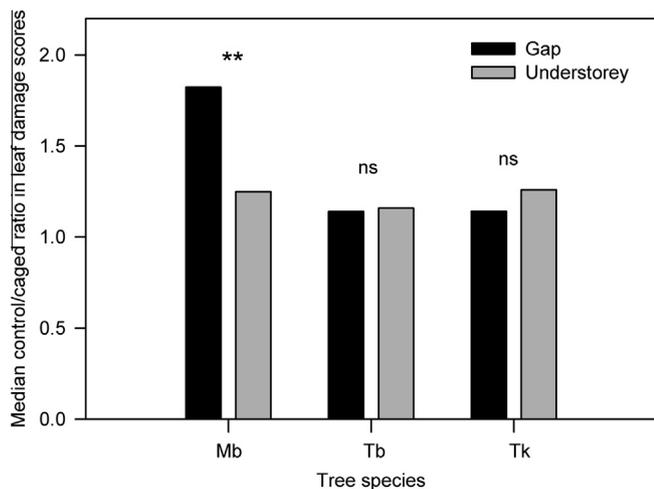
**Table 3**

Static damage to leaves produced in canopy gaps of *Microberlinia bisulcata* (Mb), *Tetraberlinia bifoliolata* (Tb) and *T. korupensis* (Tk) tree seedlings at Korup, Cameroon, in three successive time intervals (DW<sub>1</sub>, D<sub>2</sub>, and W<sub>2</sub>; refer to Fig. 1). Within-species differences between caged and control treatments were tested using a non-parametric approach (Mann-Whitney U-test, one-tailed, control > caged). Control medians of *M. bisulcata* not sharing the same small letters in that time interval with either *Tetraberlinia* species are significantly different at  $P \leq 0.05$  (see Results for statistics). Leaves were scored at the end of each interval: a value of 1 (0–5% damaged) was the lower bound and a value of 5 (75–100% damaged) was the upper bound. (Scores of 2, 3, and 4 correspond to leaves with 5–20%, 20–50%, and 50–75% of leaf area missing).  $n$  = number of seedlings.

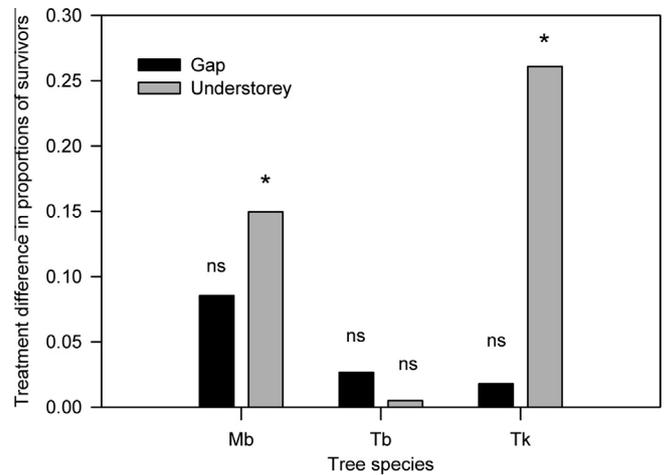
	Control				Caged				U	P
	Median	Mean	Skew	n	Median	Mean	Skew	n		
DW <sub>1</sub>										
Mb	<sup>a</sup> 2.05	2.16	1.01	75	1.00	1.32	2.89	97	1190.5	< 0.001
Tb	<sup>b</sup> 1.30	1.38	1.26	39	1.00	1.13	1.89	40	430.5	< 0.001
Tk	<sup>b</sup> 1.00	1.28	1.93	25	1.00	1.05	3.41	27	229.0	0.008
D <sub>2</sub>										
Mb	<sup>a</sup> 1.33	1.59	1.25	66	1.00	1.17	3.38	95	1727.5	< 0.001
Tb	<sup>b</sup> 1.00	1.32	1.49	34	1.00	1.04	5.56	38	402.5	< 0.001
Tk	<sup>a</sup> 1.25	1.40	1.90	23	1.00	1.10	2.86	28	209.0	0.005
W <sub>2</sub>										
Mb	<sup>a</sup> 2.15	2.34	0.70	31	1.15	1.59	1.71	74	752.5	0.002
Tb	<sup>b</sup> 1.25	1.55	1.97	25	1.00	1.11	1.95	34	262.5	0.002
Tk	<sup>a</sup> 2.00	1.98	0.32	17	1.05	1.68	1.47	20	133.5	0.126



**Fig. 4.** Insect herbivory, expressed as the proportion of seedlings' leaves which were clearly damaged in this way, grouped according to whether they had (a) <50% or (b) ≥50% missing leaf area on *Microberlinia bisulcata* (Mb), *Tetraberlinia bifoliolata* (Tb) and *T. korupensis* (Tk), in gaps for the herbivore treatments (caged vs. control) at Korup. Symbols are means with their 95% confidence limits as bars. Sample sizes (range 20–88 seedlings) are given in Appendix M.



**Fig. 5.** Test of the Plant Vigor Hypothesis (PVH) using damage ratios for leaves of *Microberlinia bisulcata* (Mb), *Tetraberlinia bifoliolata* (Tb) and *T. korupensis* (Tk) at Korup. Significance levels are differences between the treatments between canopy types: \*\*,  $P \leq 0.005$ ; ns,  $P > 0.05$ . Sample sizes (ranges = 7–30 canopy type locations) are given in Appendix M.



**Fig. 6.** Test of the Limiting Resource Model (LRM) using absolute differences in survivorship between control and caged seedlings, within each canopy type, of *Microberlinia bisulcata* (Mb), *Tetraberlinia bifoliolata* (Tb) and *T. korupensis* (Tk) at Korup. Significance levels are for differences between the treatments within canopy type: \*,  $P \leq 0.05$ ; ns,  $P > 0.05$ . Sample sizes (range 23–100 seedlings) are given in Appendix M.

greater susceptibility of seedlings to insect herbivores in gaps than under closed forest canopy has been reported from both temperate and tropical sites, especially for long-lived tree species whose seedlings are at the low end of the shade-tolerance spectrum ('light-demanding') like *M. bisulcata* (Shure and Wilson, 1993; Chacon and Armesto, 2006; Norghauer et al., 2008; Salgado-Luarte and Gianoli, 2010).

We are unaware of any other tropical field study that has physically excluded insects under natural conditions in both canopy gaps and understorey environments of forests. In Panama Sagers and Coley (1995) reported increased growth rates of the shrub, *Psychotria horizontalis*, when caged in gaps, as did Pearson et al. (2003) for leaf area production on *Miconia argentea*. For the Peruvian Amazon, Fine et al. (2004) reported increased tree seedling growth rates in terms of leaf area (but not height) for 11 clay-soil specialists, yet no benefit of protection for nine congeneric white-sand specialists when caged in comparable light conditions between soil types. Nor was growth improved for an insecticide-treated shrub (*Clidemia hirta*) in Costa Rican forest tested in different light habitats (DeWalt et al., 2004). Several non-exclusion studies have quantified leaf herbivory on tree seedlings, as well as their growth dynamics, in various forests in the Neotropics and South-East Asia, and all of them concluded that there was a negligible impact of herbivory on species' seedling growth, even when growing in gaps (Coley, 1983; Angulo-Sandoval and Aide, 2000; Howlett and Davidson, 2001; Massey et al., 2006; Eichhorn et al., 2010). We would have concluded the same for *M. bisulcata* and *T. bifoliolata* had we likewise relied upon correlations between leaf damage and growth instead of manipulating seedling exposure to herbivores. Our study shows that such observed correlations may underestimate the impact of insect herbivores on the performance of tree seedlings and saplings.

#### 4.3. Herbivory and survival

In the understorey, light was in limiting supply compared with gaps. Exposure to herbivory, which reduces the leaf area a plant has to capture light, was more detrimental under low- compared with high-light conditions for *M. bisulcata* and *T. korupensis*. We interpret this result as partial support for the Limiting Resource

Model (LRM, Wise and Abrahamson, 2005). It adds to broadening support for the LRM of plant species' responses to herbivory when their resources were most limiting (water, light or nutrients; Wise and Abrahamson, 2007), and to the surprisingly few studies that have investigated light as the limiting resource in tropical forests in tests of the LRM (Dirzo, 1984; Blundell and Peart, 2001; Norghauer et al., 2008). By contrast, the third species studied, *T. bifoliolata*, survived best and equally well in both treatments in both light environments. This suggests that not only is it highly resistant to being eaten, but also that the leaf physiology of its seedlings confers a strong ability to persist under low light levels. The latter could be achieved by having evolved a low 'whole-plant-light-compensation-point' (Baltzer and Thomas, 2007).

#### 4.4. Implications for regeneration dynamics at Korup

The general near-absence of above-ground growth in the understorey indicates that newly established seedlings most likely require at least one canopy disturbance above or near them to obtain enough light resources to quickly grow into large saplings (defined here as >1 cm stem diameter; Newbery et al., 2010). Differences in shade-tolerance among species are thought to generally decline with ontogeny, however (Poorter et al., 2005). At Korup, after the large seedling stage, shade-tolerance of *M. bisulcata* improves rapidly because saplings and pole-size stems can effectively track the vertical profile and shifting pockets of light in the forest canopy via its multiple, plagiotropic branching (Newbery et al., 2010; J. M. Norghauer, pers. observ.).

The starting size hierarchy of *T. bifoliolata* > *T. korupensis* > *M. bisulcata* in terms of seedling heights was maintained through the first 2 years in the understorey, and mirrored their survivorship there. This matches the ranking seen over the same time-frame in a separate 7-year demographic survey of the three species after a joint masting event at Korup in 1995 (Newbery et al., 2006b), and supports the view that 'shade-tolerance' in seedlings is perhaps best understood as a strategy to persist and thereby increase the probability of being present when a new canopy opening occurs nearby (Canham, 1989; Kitajima, 1994). For *M. bisulcata*, the negative overall growth in leaf numbers in the understorey is consistent with its low tolerance of prolonged shade c. 2.5 years after establishment. Without more light, these seedlings—less so when caged though—were declining towards their death, gradually losing more leaflets and leaves over the second wet season, either to herbivores or shed to offset accumulating respiration costs.

Furthermore, had we measured total leaf area on plants, then the impact of herbivores on *M. bisulcata* might have been revealed as being stronger since a decreased ability to intercept light would lower persistence after gaps closed (Newbery et al., 2010). Accordingly, herbivory should further alter the distributions and abundance patterns of *M. bisulcata* saplings along the forest light gradient beyond the patchiness already generated by the local regime of canopy gap-disturbances and variable dispersal shadows. Elsewhere, a similar conclusion was recently reached for the impact of herbivory on two temperate trees, *Aristotelia chilensis* and *Embothrium coccineum*, whose seedlings are 'light-demanding' and have difficulty regrowing leaves under closed-canopy forest conditions (Salgado-Luarte and Gianoli, 2010, 2011). However, we cannot say whether herbivory affected root growth, or possibly even the ectomycorrhizas, of these Korup tree species (reviewed by Gehring and Whitham (1994)).

#### 4.5. Herbivore impacts and tree coexistence

We have empirically shown that while light availability is the primary limitation to the growth of all three species' new seedlings, another substantial limitation to the recruitment of *M. bisul-*

*cata* is herbivory by leaf-chewing insects. This species' local dominance in the main canopy at Korup is obviously not enhanced by the higher impact in gaps compared to that experienced by the two *Tetraberlinia* species. Regeneration in the subcanopy over the recent decades has been far better for the *Tetraberlinia* species than for *M. bisulcata* (Newbery et al., 1988, 2013). Therefore, under the current conditions of forest dynamics, we suggest that insect herbivores exercise an 'equalizing' force on this community (*sensu* Chesson, 2000), because they function to reduce early differences in plant fitness among the three species that would continue to be expressed were the herbivores absent.

We further suggest that the key functional leaf traits that enabled *M. bisulcata* to attain its dominance as adults in the forest via fast tree growth in stems >10 cm diameter (Newbery et al., 2013) may have been traded-off against low resistance to herbivores at the seedling stage (Coley et al., 1985). Recruitment of *M. bisulcata* saplings is thought to preferentially occur during periods of infrequent drought as the understorey becomes better lit (Newbery et al., 2004). If herbivore pressure were reduced during those also drier times, as we have shown for the dry season, this would further facilitate the regeneration of *M. bisulcata*. Such an 'ontological trade-off' between resistance and performance traits might, therefore, help explain the contrasting current population structures of *M. bisulcata* (modal) and the two *Tetraberlinia* species (reverse 'J').

In treefall gaps, seedling growth rates are an important determinant of successful recruitment into larger size-classes to avoid being shaded by faster-growing neighbours, to lessen mortality risks under closed forest conditions, and to more quickly reach the canopy to attain maturity and reproduce (Denslow, 1987; Canham, 1989; Connell, 1989; Sullivan, 2003; Nair, 2007). Important differential impacts of herbivores on co-occurring species' population dynamics can arise from differential resistance to their attacks (Kulman, 1971; Hartshorn, 1978; Dirzo, 1984; Marquis, 2005; Maron and Crone, 2006). For a competitively superior species like *M. bisulcata*, this should weaken its ability to dominate for certain periods until conditions in the forest change in way that lessens (or removes) this bi-trophic limitation from insect herbivores.

## 5. Conclusions and implications for management of *M. bisulcata*

The tree species that was most affected by herbivores is also a critically endangered high-value timber endemic to SW Cameroon and SE Nigeria (IUCN category A1c + 2c). In this region it is locally known as 'zingana' (Aubréville, 1970), and more widely in central Africa (including *Microberlinia brazzavillensis*) as zebano, or true zebrawood (Chudnoff, 1984). But unlike other, better known tropical timbers, *M. bisulcata* has a very small range, relatively poor dispersal ability (ballistic), and very short-lived seeds. As far as we know, Korup contains the only protected populations of *M. bisulcata*. From a conservation perspective and given its low natural regeneration under current conditions, concerted efforts should be made to search and protect other remnant groves of *M. bisulcata* outside of Korup. From a management perspective, our results suggest that because *M. bisulcata* seedlings are capable of very fast growth in gaps, transplantation or manual seeding into gaps could help restore degraded populations in unprotected and logged forests, especially if such an approach were complemented by early protection of seedlings from insect herbivores. Doing so would accelerate the growth and recruitment of seedlings into saplings, and thereby increase their tree longevity as larger saplings gained better access to light. Interestingly, too, this tree species appears not to be susceptible to insect herbivores when planted in a cleared-forest setting (D. M. Newbery, G. B. Chuyong, unpublished data), a result supported by the low attack it sustained in drier

periods in a forest setting (present work). This coupled to its large, widespread root system as the tree grows, and its distinct phosphorus recycling ability, suggests that *M. bisulcata* may hold considerable promise for forest restoration and agroforestry systems in central Africa.

## Acknowledgements

We thank the Conservator of Korup National Park, P. Ndongmo, and the Ministries of Forestry and Wildlife (MINFOF) and Scientific Research and Innovation (MINRESI) in Cameroon for granting us research permission; G. B. Chuyong and R. Kometa of the University of Buea for logistic support; and S. Njibile and C. Ohka for their excellent assistance in the forest.

## Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.08.029>.

## References

- Agresti, A., 2007. An introduction to categorical data analysis. John Wiley & Sons.
- Angulo-Sandoval, P., Aide, T.M., 2000. Effect of plant density and light availability on leaf damage in *Manilkara bidentata* (Sapotaceae). *J. Trop. Ecol.* 16, 447–464.
- Aubréville, A., 1970. Flore du Cameroun. Vol. 9. Légumineuses-Césalpinioidées, Muséum National d'Histoire Naturelle, Paris.
- Baltzer, J.L., Thomas, S.C., 2007. Determinants of whole-plant light requirements in Bornean rain forest tree saplings. *J. Ecol.* 95, 1208–1221.
- Bazzaz, F.A., Pickett, S.T.A., 1980. Physiological ecology of tropical succession – a comparative review. *Annu. Rev. Ecol. Syst.* 11, 287–310.
- Blundell, A.G., Peart, D.R., 2001. Growth strategies of a shade-tolerant tropical tree: the interactive effects of canopy gaps and simulated herbivory. *J. Ecol.* 89, 608–615.
- Boege, K., 2004. Induced responses in three tropical dry forest plant species – direct and indirect effects on herbivory. *Oikos* 107, 541–548.
- Canham, C.D., 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70, 548–550.
- Carson, W.P., Root, R.B., 2000. Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecol. Monogr.* 70, 73–99.
- Chacon, P., Armesto, J.J., 2006. Do carbon-based defences reduce foliar damage? Habitat-related effects on tree seedling performance in a temperate rainforest of Chiloe Island, Chile. *Oecologia* 146, 555–565.
- Chazdon, R.L., Pearcy, R.W., Lee, D.W., Fetcher, N., 1996. Photosynthetic responses of tropical forest plants to contrasting light environments. In: Mulkey, S.S., Chazdon, R.L., Smith, A.P. (Eds.), *Tropical forest plant ecophysiology*. Chapman & Hall, New York, USA, pp. 5–55.
- Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31, 343–366.
- Chudnoff, M., 1984. Tropical timbers of the world. *Agricultural Handbook Number 607*. United States Department of Agriculture, Forest Service, USA.
- Coley, P.D., 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* 53, 209–233.
- Coley, P.D., Barone, J.A., 1996. Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* 27, 305–335.
- Coley, P.D., Kursar, T.A., 1996. Anti-herbivore defenses of young tropical leaves: physiological constraints and ecological trade-offs. In: Mulkey, S.S., Chazdon, R.L., Smith, A.P. (Eds.), *Tropical forest plant ecophysiology*. Chapman & Hall, New York, USA, pp. 305–336.
- Coley, P.D., Bryant, J.P., Chapin, F.S., 1985. Resource availability and plant antiherbivore defense. *Science* 230, 895–899.
- Connell, J.H., 1989. Some processes affecting the species composition in forest gaps. *Ecology* 70, 560–562.
- Cruz, M., Dirzo, R., 1987. A survey of the standing levels of herbivory in seedlings from a Mexican rain-forest. *Biotropica* 19, 98–106.
- Dalling, J.W., Burslem, D.F.R.P., 2005. Role of life-history trade-offs in the equalization and differentiation of tropical tree species. In: Burslem, D.F.R.P., Pinard, M.A., Hartley, S.E. (Eds.), *Biotic interactions in the tropics: their role in the maintenance of species diversity*. Cambridge University Press, Cambridge, UK, pp. 65–88.
- Dalling, J.W., Pearson, T.R.H., Ballesteros, J., Sanchez, E., Burslem, D.F.R.P., 2009. Habitat partitioning among neotropical pioneers: a consequence of differential susceptibility to browsing herbivores? *Oecologia* 161, 361–370.
- Day, R.W., Quinn, G.P., 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* 59, 433–463.
- Denslow, J.S., 1987. Tropical rain-forest gaps and tree species-diversity. *Annu. Rev. Ecol. Syst.* 18, 431–451.
- DeWalt, S.J., Denslow, J.S., Ickes, K., 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology* 85, 471–483.
- Dirzo, R., 1984. Herbivory: a phytocentric overview. In: Dirzo, R., Sarukhan, J. (Eds.), *Perspectives on plant population ecology*. Sinauer Associates Inc., Sunderland, USA, pp. 141–165.
- Dyer, L.A., Letourneau, D.K., Chavarria, G.V., Amoretti, D.S., 2010. Herbivores on a dominant understory shrub increase local plant diversity in rain forest communities. *Ecology* 91, 3707–3718.
- Eichhorn, M.P., Compton, S.G., Hartley, S.E., 2006. Seedling species determines rates of leaf herbivory in a Malaysian rain forest. *J. Trop. Ecol.* 22, 513–519.
- Eichhorn, M.P., Nilus, R., Compton, S.G., Hartley, S.E., Burslem, D.F.R.P., 2010. Herbivory of tropical rain forest tree seedlings correlates with future mortality. *Ecology* 91, 1092–1101.
- Fine, P.V.A., Mesones, I., Coley, P.D., 2004. Herbivores promote habitat specialization by trees in amazonian forests. *Science* 305, 663–665.
- Galwey, N.W., 2006. Introduction to mixed modelling: beyond regression and analysis of variance. John Wiley & Sons, Ltd., West Sussex, UK.
- Garcia-Guzman, G., Dirzo, R., 2001. Patterns of leaf-pathogen infection in the understory of a Mexican rain forest: Incidence, spatiotemporal variation, and mechanisms of infection. *Am. J. Bot.* 88, 634–645.
- Gartlan, J.S., Newbery, D.M., Thomas, D.W., Waterman, P.G., 1986. The influence of topography and soil-phosphorus on the vegetation of Korup forest reserve, Cameroon. *Vegetatio* 65, 131–148.
- Gehring, C.A., Whitham, T.G., 1994. Interactions between aboveground herbivores and the mycorrhizal mutualists of plants. *Trends Ecol. Evol.* 9, 251–255.
- Gendron, F., Messier, C., Comeau, P.G., 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. *Agr. Forest Meteorol.* 92, 55–70.
- Green, J.J., Newbery, D.M., 2001a. Light and seed size affect establishment of grove-forming ectomycorrhizal rain forest tree species. *New Phytol.* 151, 271–289.
- Green, J.J., Newbery, D.M., 2001b. Shade and leaf loss affect establishment of grove-forming ectomycorrhizal rain forest tree species. *New Phytol.* 151, 291–309.
- Gross, N.D., Torti, S.D., Feener, D.H., Coley, P.D., 2000. Monodominance in an African rain forest: Is reduced herbivory important? *Biotropica* 32, 430–439.
- Hancock, G.R., Klockars, A.J., 1996. The quest for alpha: Developments in multiple comparison procedures in the quarter century since Games (1971). *Rev. Educ. Res.* 66, 269–306.
- Hartshorn, G.S., 1978. Tree falls and forest dynamics. In: Tomlinson, P.B., Zimmermann, M.H. (Eds.), *Tropical trees as living systems*. Cambridge University Press, London, UK, pp. 617–638.
- Howe, H.F., 1990. Survival and growth of juvenile *Virola-surinamensis* in Panama – effects of herbivory and canopy closure. *J. Trop. Ecol.* 6, 259–280.
- Howlett, B.E., Davidson, D.W., 2001. Herbivory on planted dipterocarp seedlings in secondary logged forests and primary forests of Sabah, Malaysia. *J. Trop. Ecol.* 17, 285–302.
- Ickes, K., Paciorek, C.J., Thomas, S.C., 2005. Impacts of nest construction by native pigs (*Sus scrofa*) on lowland Malaysian rain forest saplings. *Ecology* 86, 1540–1547.
- Jackson, R.V., Bach, C.E., 1999. Effects of herbivory on growth and survival of seedlings of a rainforest tree, *Alphitonia whitei* (Rhamnaceae). *Aust. J. Ecol.* 24, 278–286.
- Kitajima, K., 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98, 419–428.
- Kitajima, K., Poorter, L., 2008. Functional basis for resource partitioning by tropical trees. In: Carson, W.P., Schnitzer, S.A. (Eds.), *Tropical forest community ecology*. Blackwell Publishing Ltd., Oxford, UK, pp. 160–181.
- Kulman, H.M., 1971. Effects of insect defoliation on growth and mortality of trees. *Annu. Rev. Entomol.* 16, 289–323.
- Maron, J.L., Crone, E., 2006. Herbivory: effects on plant abundance, distribution and population growth. *P. Roy. Soc. Lond. B.* 273, 2575–2584.
- Marquis, R.J., 2005. Impacts of herbivores on tropical plant diversity. In: Burslem, D.F.R.P., Pinard, M.A., Hartley, S.E. (Eds.), *Biotic interactions in the tropics: their role in the maintenance of species diversity*. Cambridge University Press, Cambridge, UK, pp. 328–365.
- Massey, F.P., Massey, K., Press, M.C., Hartley, S.E., 2006. Neighbourhood composition determines growth, architecture and herbivory in tropical rain forest tree seedlings. *J. Ecol.* 94, 646–655.
- Messier, C., Puttonen, P., 1995. Spatial and temporal variation in the light environment of developing Scots pine stands – the basis for a quick and efficient method of characterizing light. *Can. J. Forest Res.* 25, 343–354.
- Nair, K.S.S., 2007. Tropical forest insect pests: ecology, impact and management. Cambridge University Press, New York.
- Newbery, D.M., Alexander, I.J., Thomas, D.W., Gartlan, J.S., 1988. Ectomycorrhizal rain-forest legumes and soil-phosphorus in Korup National Park, Cameroon. *New Phytol.* 109, 433–450.
- Newbery, D.M., van der Burgt, X.M., Moravie, M.A., 2004. Structure and inferred dynamics of a large grove of *Microberlinia bisulcata* trees in central African rain forest: the possible role of periods of multiple disturbance events. *J. Trop. Ecol.* 20, 131–143.
- Newbery, D.M., Chuyong, G.B., Zimmermann, L., 2006a. Mast fruiting of large ectomycorrhizal African rain forest trees: importance of dry season intensity, and the resource-limitation hypothesis. *New Phytol.* 170, 561–579.

- Newbery, D.M., Chuyong, G.B., Zimmermann, L., Praz, C., 2006b. Seedling survival and growth of three ectomycorrhizal caesalpiniaceous tree species in a Central African rain forest. *J. Trop. Ecol.* 22, 499–511.
- Newbery, D.M., Praz, C.J., van der Burgt, X.M., Norghauer, J.M., Chuyong, G.B., 2010. Recruitment dynamics of the grove-dominant tree *Microberlinia bisulcata* in African rain forest: extending the light response versus adult longevity trade-off concept. *Plant Ecol.* 206, 151–172.
- Newbery, D.M., van der Burgt, X.M., Worbes, M., Chuyong, G.B., 2013. Transient dynamics in a central African rain forest. *Ecol. Monogr.* 83, 339–382.
- Norghauer, J.M., Newbery, D.M., in press. Herbivores differentially limit the seedling growth and sapling recruitment of two dominant rain forest trees. *Oecologia*.
- Norghauer, J.M., Newbery, D.M., 2011. Seed fate and seedling dynamics after masting in two African rain forest trees. *Ecol. Monogr.* 81, 443–468.
- Norghauer, J.M., Malcolm, J.R., Zimmerman, B.L., 2008. Canopy cover mediates interactions between a specialist caterpillar and seedlings of a neotropical tree. *J. Ecol.* 96, 103–113.
- Osunkoya, O.O., Ash, J.E., Graham, A.W., Hopkins, M.S., 1993. Growth of tree seedlings in tropical rain forests of North Queensland, Australia. *J. Trop. Ecol.* 9, 1–18.
- Payne, R.W., Harding, S.A., Murray, D.A., Soutar, D.M., Baird, D.B., Glaser, A.I., Channing, I.C., Welham, S.J., Gilmour, A.R., Thompson, R., Webster, R., 2009. Genstat Release 12 Reference Manual. VSN International, Hemel Hempstead.
- Pearson, T.R., Burslem, D.F.R.P., Goeriz, R.E., Dalling, J.W., 2003. Interactions of gap size and herbivory on the establishment, growth and survival of three species of neotropical pioneer trees. *J. Ecol.* 91, 785–796.
- Plath, M., Mody, K., Potvin, C., Dorn, S., 2011. Establishment of native tropical timber trees in monoculture and mixed-species plantations: Small-scale effects on tree performance and insect herbivory. *Forest Ecol. Manage.* 261, 741–750.
- Poorter, L., Bongers, F., Sterck, F.J., Woll, H., 2005. Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. *J. Ecol.* 93, 256–267.
- Price, P.W., 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62, 244–251.
- Quinn, G.P., Keough, M.J., 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.
- Sagers, C.L., Coley, P.D., 1995. Benefits and costs of defense in a neotropical shrub. *Ecology* 76, 1835–1843.
- Salgado-Luarte, C., Gianoli, E., 2010. Herbivory on temperate rainforest seedlings in sun and shade: resistance, tolerance and habitat distribution. *Plos ONE* 5, e11460.
- Salgado-Luarte, C., Gianoli, E., 2011. Herbivory may modify functional responses to shade in seedlings of a light-demanding tree species. *Funct. Ecol.* 25, 492–499.
- Shure, D.J., Wilson, L.A., 1993. Patch-size effects on plant phenolics in successional openings of the southern appalachians. *Ecology* 74, 55–67.
- Sork, V.L., 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. *Ecology* 68, 1341–1350.
- Sullivan, J.J., 2003. Density-dependent shoot-borer herbivory increases the age of first reproduction and mortality of neotropical tree saplings. *Oecologia* 136, 96–106.
- Swamy, V., Terborgh, J.W., 2010. Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. *J. Ecol.* 98, 1096–1107.
- Wise, M.J., Abrahamson, W.G., 2005. Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory. *Oikos* 109, 417–428.
- Wise, M.J., Abrahamson, W.G., 2007. Effects of resource availability on tolerance of herbivory: A review and assessment of three opposing models. *Am. Nat.* 169, 443–454.