Oecologia (2014) 174:459–469
DOI 10.1007/s00442-013-2769-6

PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Herbivores differentially limit the seedling growth and sapling recruitment of two dominant rain forest trees

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Received: 6 February 2013 / Accepted: 30 August 2013 / Published online: 26 September 2013

Abstract Resource heterogeneity may influence how plants are attacked and respond to consumers in multiple ways. Perhaps a better understanding of how this interaction might limit sapling recruitment in tree populations may be achieved by examining species' functional responses to herbivores on a continuum of resource availability. Here, we experimentally reduced herbivore pressure on newly established seedlings of two dominant masting trees in 40 canopy gaps, across c. 80 ha of tropical rain forest in central Africa (Korup, Cameroon). Mesh cages were built to protect individual seedlings, and their leaf production and changes in height were followed for 22 months. With more light, herbivores increasingly prevented the less shade-tolerant *Microberlinia bisulcata* from growing as tall as it could and producing more leaves, indicating an undercompensation. The more shade-tolerant *Tetraberlinia bifoliolata* was much less affected by herbivores, showing instead near to full compensation for leaf numbers, and a negligible to weak impact of herbivores on its height growth. A stage-matrix model that compared control and caged populations lent evidence for a stronger impact of herbivores on the long-term population dynamics of *M. bisulcata* than *T. bifoliolata*. Our results suggest that insect herbivores can contribute to the local coexistence of two abundant tree species at Korup by disproportionately suppressing sapling recruitment of the faster-growing dominant via undercompensation across the light gradient created by canopy disturbances. The functional patterns we have documented here are consistent with current theory, and, because gap formations are integral to forest regeneration, they may be more widely applicable in other tropical forest communities. If so, the interaction between life-history and herbivore impact across light gradients may play a substantial role in tree species coexistence.

Keywords Africa · Canopy gaps · Herbivory · Insects · Tropics

Introduction

Insects that eat plants can reduce the latter's growth, survival, and fecundity, but their possible contributing role to the dynamics of tree populations in forest communities is controversial, and still far from clear (Crawley 1989; Blundell and Peart 2004; Halpern and Underwood 2006; Maron and Crone 2006; Carson et al. 2008). In particular, the negative effects of invertebrate herbivory, often subtle and difficult to detect, might be problematic for long-lived canopy species when they are both vulnerable and abundant as new seedlings, and later too as saplings (Kulman 1971; Clark and Clark 1985; Howe et al. 1985; Coley and Barone 1996; Sullivan 2003; Nair 2007), especially in nutrient-poor tropical rain forests characterized by low soil fertility, where it is costly to replace eaten tissues (Janzen 1974; Coley et al. 1985; Givnish 1999).

Potentially vigorously growing plants are thought to be preferred by insect herbivores ('Plant Vigor Hypothesis', Price 1991). However, the damage caused by these herbivores may or may not decrease their host-plant's fitness

Communicated by Dave Peart.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-013-2769-6) contains supplementary material, which is available to authorized users.

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depending on the availability of scarce resources in its environment which could influence a plant's tolerance to attack ('Limiting Resource Hypothesis'; Wise and Abrahamson 2007). And both aspects of these interactions can differ between species and likely also change with ontogeny (Boege and Marquis 2005; Nair 2007). In contrast to these plastic responses within populations, among species a positive correlation is expected between the intensity of herbivory and plant performance (Coley 1987), especially if intrinsic plant growth rates are used (i.e., those measured in the absence of herbivory). This is because of a physiological trade-off between the evolved capacity for faster growth under favorable resource conditions at the cost of lower investment in constitutive defenses ('Resource Availability Hypothesis'; Coley et al. 1985; reviewed recently by Endara and Coley 2011). At the community level, several lines of theory further suggest that plant diversity is maintained if there is a greater negative impact of herbivory, in particular by generalists, on the competitively dominant species than upon the less dominant species (Pacala and Crawley 1992; Holt and Lawton 1994 and references therein; see recent reviews by Carson et al. 2008; Viola et al. 2010; and studies by Dyer et al. 2010; Clark et al. 2012).

Light is the scarcest resource for new seedlings in the understory of tropical rain forests (<1–3 % full sun), except at places where above-average PAR (photosynthetically active radiation) is temporally admitted by small-scale canopy disturbances created by trees snapping or tipping over, or losing parts of their crowns (Chazdon et al. 1996). These 'canopy gaps' create a continuous, shifting mosaic of patches of competing vegetation, where height growth is of selective advantage for a tree species (Denslow 1987; Kellner et al. 2009). Being a fundamental feature of many forests in general, gaps likely affect the population dynamics and species composition of not only pioneer trees but also those species varying widely in shade tolerance early in their ontogeny (Hartshorn 1978; Canham 1989; Chazdon et al. 1996; Wright et al. 2003). Nevertheless, because increased light promotes vigorous plant growth, gaps are 'rich islands of food' for invertebrate herbivores (Richards and Coley 2007). To better understand how the latter might limit tree species' recruitment, and perhaps promote their coexistence, it seems their impact in and around gaps cannot be ignored (Hartshorn 1978; Connell 1989; e.g., Pearson et al. 2003; Norghauer et al. 2008; Eichhorn et al. 2010).

In reality, moreover, light levels will vary both within and among gaps, and grade into the surrounding forest matrix (Canham 1989; Chazdon et al. 1996). So perhaps a better way to investigate the impact of herbivores on plant growth rates is by considering light resources on a continuum, as shown in Fig. 1. This suggests multiple responses in populations of plants—possibly shifting the relative resistances and competitive abilities of co-existing species (Hartshorn 1978; Connell 1989). In Fig. 1a, freedom from herbivore attack does not improve growth of seedlings because they are well defended against herbivores (when present), or they are able to replace any eaten tissues (or a combination of these responses). But if herbivores attack the more vigorously growing seedlings in a population (Fig. 1c), as suggested by the Plant Vigor Hypothesis, then their negative impact in the absence of mechanisms to compensate for lost tissues should be greater at higher rather than lower light levels (all other factors being equal). Because individuals fail to grow at their maximum intrinsic rate, this leads to a general negative impact due to this undercompensation (= '−' symbols). There is then greater variation in performance among individuals in the population than is seen in Fig. 1b; for which a difference in the negative impact on growth from herbivory does not change with increasing light availability. Three other, more subtle, outcomes might occur due to increasing tolerance to damage and/or decreased susceptibility with changing light levels (Fig. 1d–f). Any of them can result in a reduced negative impact of herbivory such that plant growth becomes the same as without herbivores at higher light levels that facilitate compensation in growth (Fig. 1d), as suggested by the limiting resource model. Alternatively, there is a positive impact of herbivory in the form of overcompensation (= '+' symbols) for damage at higher light levels with undercompensation at lower light levels (Fig. 1e); or, again, overcompensation occurs at only lower light levels while undercompensation prevails at higher light levels (Fig. 1f). The functional forms of Fig. 1 may have important consequences for the dynamics of long-lived tree species because, while 'fast-growers' are in the minority as seedlings, they usually contribute disproportionately strongly to sapling recruitment (which in turn determines the potential composition of the canopy). Therefore, a better understanding of functional growth responses to herbivory could yield insight into 'top–down' limitations on sapling recruitment, and they should vary predictably among species differing in key life-history traits (Coley et al. 1985). Surprisingly, such responses have gone mostly untested in forest trees (Hawkes and Sullivan 2001; Boege and Marquis 2005; Marquis 2005).

A suitable place to investigate these interactions is in the ancient forest of Korup National Park (KNP) in central Africa. Here, the huge dominant *Microberlinia bisulcata* A. Chev. (Caesalpiniaceae) has formed a large 272-ha grove with two co-dominating, though more shade-tolerant, canopy trees [*Tetraberlinia bifoliolata* (Harms) Haumann and *T. korupensis* Wieringa (also Caesalpiniaceae)] (see Newbery et al. 2004, 2013). Earlier experiments at Korup by Green and Newbery (2001) revealed that, among nine more common species tested under increasing levels of light availability (1.3–36 % PAR), *M. bisulcata* had the lowest above-ground biomass in the field relative to herbivore-free

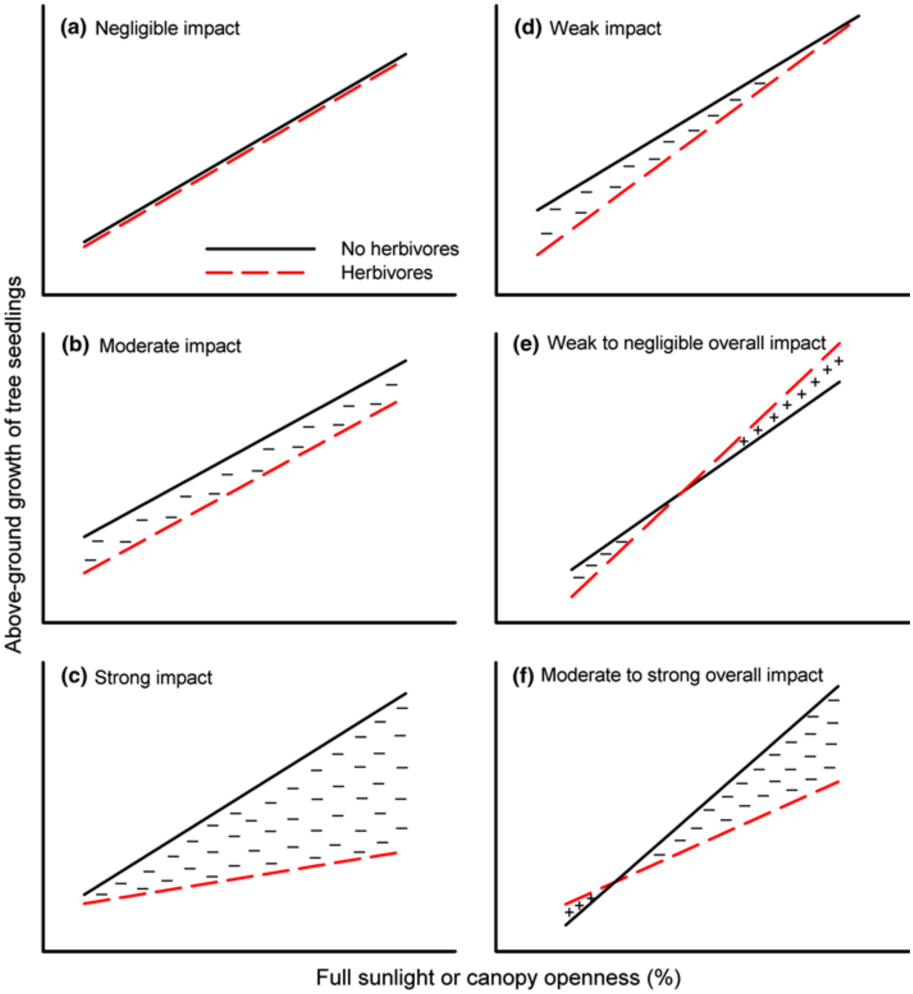

Fig. 1 Hypothesized differential impacts of herbivory on plant growth as a function of available light. The impact of herbivory on growth is estimated from the size of the area between the two lines, which are plant responses in the field for individuals with and without their herbivores, across the range of light levels experienced by the population at a site. A negative impact on plant growth (denoted by '−') results from undercompensation in response to herbivory; a positive impact (denoted by '+') indicates an overcompensation to herbivory

conditions in the nursery, leading the authors to hypothesize a relatively strong role for insect herbivores limiting the early tree growth of this species, and a lesser role for *T. bifoliolata* and *T. korupensis*. To test this hypothesis, we protected naturally established seedlings of *M. bisulcata* and *T. bifoliolata*, one of the *Tetraberlinia* species, from attack by above-ground herbivores in many gaps. We had two questions: (1) do *M. bisulcata* and *T. bifoliolata* have functional growth responses to herbivory that are consistent with the Plant Vigor Hypothesis? and (2) what are the possible demographic implications of these different impacts of herbivory on seedling growth for sapling recruitment in each species' population?

Materials and methods

Study site and species

The experiment was done in moist lowland tropical forest in the south of KNP (SW Cameroon) in the 82.5-ha permanent 'P-plot' set-up in 1990–1991 (5°10′N, 8°52′E; Newbery et al. 2004). The climate is very wet but punctuated by a few very dry months (Fig. 2). Annual rainfall exceeds 5,000 mm and drains well on the forest's sandy soils which are nutrient-poor in phosphorus and potassium (Newbery et al. 2006). Nevertheless, in the P-plot, 186 tree species were found with 20 or more stems $\geq$10 cm diameter in 1991, and in the 2005 plot enumeration, the relative abundance of *M. bisulcata* and *T. bifoliolata* amongst stems $\geq$50 cm in diameter was 18.3 and 10.1 %, respectively. These large trees amounted to 38.8 and 10.6 %, respectively, of the basal area of the overstory tree community (Newbery et al. 2013). New seedlings of *M. bisulcata* have 3–6 pinnately compound leaves, while *T. bifoliolata* has two leaves each with two leaflets (a "leaflet" = a "leaf" in analyses; Norghauer and Newbery 2011). Both species become established in the mid-to-late wet season from ballistically dispersed seeds in masting events 2–3 years apart (Green and Newbery 2001; Newbery et al. 2006).

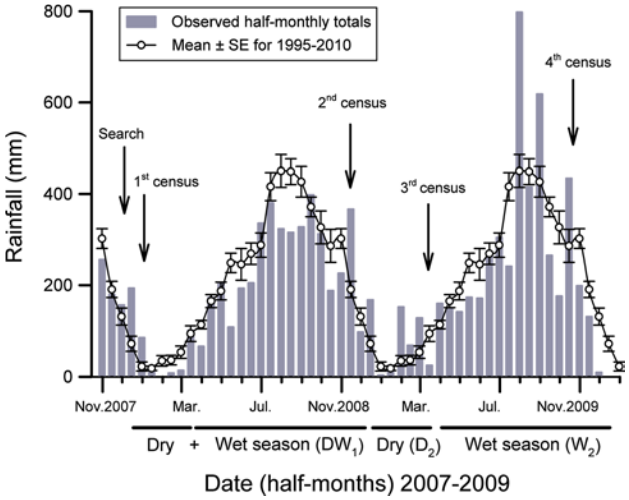

Fig. 2 Seasonal distribution of precipitation over the time-course of the experiment. Also shown are long-term means of monthly rainfall sums (see Newbery et al. 2006). The first census interval included the latter part of the 2007–2008 dry season and most of the 2008 wet season (DW_1); the second interval included all of the 2008–2009 dry season (D_2); the third interval was primarily the 2009 wet season (W_2)

Experimental design and installation

To control for prior exposure to herbivores, and possible size-/age-related confounding effects, we used only wild, newly established seedlings from the concurrent 2007 masting of *M. bisulcata* and *T. bifoliolata* populations (Norghauer and Newbery 2011). These new seedlings can be readily distinguished from older seedlings by their non-lignified stems. Over a 1-week period (28 November 2007–4 December 2007) c. 80 ha of the rectangular P-plot were searched systematically for naturally-formed gaps with suitable seedlings (Fig. 2). These had (1) to be firmly rooted, to minimize drought stress; (2) to be 'free-to-grow', i.e., not already overtopped by neighboring plants; (3) to have their original leaves present; and (4) to be relatively damage-free (<5 % of leaf area missing). The only criterion for defining gaps was a noticeable projected opening in the canopy with signs of tree or branch fall. Of 40 gaps found suitable, 4 were amongst the largest yet mostly within 50 m of the plot boundary (see ESM resource 1).

Flagged seedlings were randomly assigned to exposure ('control') or protection from insect herbivores ('caged'), but this was done on a pair-wise basis in larger gaps to better intersperse the treatments. Protection was achieved via physical, not chemical, exclusion by building mesh cages around individual seedlings. (At KNP, the use of insecticides is prohibited.) Cages measured c. 40 × 40 × 50-cm tall, with a few cm of mesh buried to keep out ground insects. They were each supported by four bamboo posts to which the mesh was stapled. Controls had just 50 × 50-cm rooftops (sides open). Care was taken to minimize disturbance to vegetation and woody debris around seedlings during their installation: there was no weeding. The mesh type used was ECONET B (hole size 1 × 4 mm; Ludwig-Svensson, Sweden), chosen for its durability and ability to exclude leaf-chewing insects of medium body size—Lepidoptera, Orthoptera, Phasmida, and Hymenoptera—while permitting 90 % direct light transmission (82 % diffuse) and 95 % air flow (manufacturer's specifications). Given this substantial air flow, we assumed that any pathogen activity not depressed by the higher light in canopy gaps (Augspurger and Kelly 1984) was neither impeded nor promoted in mesh cages unless strictly dependent upon insect vectors.

The treatments were applied to 280 seedlings during a 1-month period (13 December 2007–13 January 2008; Fig. 2). At this time, their initial heights were measured, and their leaves counted, marked with fine nylon thread, and scored for overall missing leaf area (ESM resource 2). Before the treatments were installed, the majority (81.8 %) of these 280 seedlings still had <5 % leaf area missing; while 43 seedlings had since accrued 5 to <20 % leaf damage (occurring on 20 control and 23 caged seedlings) and just 8 seedlings had 20 to <50 % damage (3 control and 5 caged seedlings). Some untreated *M. bisulcata* seedlings (and a few *T. bifoliolata*) were left flagged to serve as potential 'replacement seedlings' in case of seedling death. Beginning on 18 December 2007, the roofs of the cages and the controls were cleaned of litter (leaves and twigs) every 5–7 days until November 2009. The litter was slipped into the cages or under the rooftops of controls.

Light measurements

On overcast days, PPFD (photosynthetic photon flux density; ×10 μmol/m^2/s) was recorded above each seedling with a quantum photon sensor (model SKP215; Skye Instruments, Powys, UK) mounted on a tripod at 1-m height (or higher for fast-growing seedlings). Another sensor (same model) was positioned at c. 25 m height above the clearing at our camp (c. 0.5 km east of the P-plot). PPFD was recorded manually at 2-min intervals, and the values later synchronized (to the nearest min) with those from the plot. These one-time measurements of %PPFD transmitted through the canopy are expected to be well correlated with the total daily mean %PPFD (see Messier and Puttonen 1995), and have been applied in tropical rain forest studies before (e.g., Nicotra et al. 1999). We could not, however, measure %PPFD at the start of the experiment because the prevailing dry season precluded the necessary overcast conditions, and many canopy trees were undergoing leaf exchange. Two sets of readings were taken: a complete set midway into the experiment (15–21

November 2008; %$PPFD_{mid}$), and a second one at the end (11–18 November 2009, survivors only; %$PPFD_{end}$). Five additional sets of light readings were taken inside and outside the treatments (control and caged) (see ESM resource 3). Used mesh material was checked for changes in light transmittance due to weathering (see ESM resource 4). For comparative purposes, hemispherical photography was used to quantify percent canopy openness (%CO) above control and caged seedlings (described in ESM resource 5).

About halfway into the experiment (mid-November 2008) no differences in either %$PPFD_{mid}$ or %CO_{mid} were detected between treatments for either species (main effects and species x treatments interaction, six P values = 0.197–0.854; see ESM resource 2). About 1 year later, light availability was reduced by 22–33 % for %$PPFD_{end}$ (less of a change for %CO_{end}); but, as before, no differences were detected between species or treatments, nor was their interaction significant (six P values = 0.242–0.854; ESM resource 2). Our in situ and ex situ checks comparing light levels inside the two different mesh structures (caged vs. control) revealed negligible differences between them (see ESM resources 3, 4).

Growth measurements

There were no significant differences in starting height and leaf numbers between the herbivory treatments (LMM, $P = 0.948$ and 0.708, respectively), or indications that treatments interacted with species ($P = 0.651$ and 0.700). Generally, seedlings of *M. bisulcata* were slightly taller, with 1–2 more leaves, than those of *T. bifoliolata* (LMM, main species effect: $F_{1,159.3} = 8.22$, $P = 0.005$; $F_{1,240.1} = 92.2$, $P \ll 0.001$, respectively; ESM resource 2).

After the treatment installation (designated census 1), seedlings were re-censused for changes in size at three later times (i.e. censuses 2–4; on 9–14 November 2008, 11–15 March 2009, and 4–10 October 2009, respectively). The aim was to have censuses close to the dry–wet season transitions to obtain intervals of wetter versus drier periods for testing the functional responses to insect herbivores (Fig. 2). This is an important consideration because the abundance and activity of some insect guilds in tropical forests is probably affected by drier conditions (Coley and Barone 1996; Nair 2007). The three census intervals corresponded to the latter half of the first dry season and most the first wet season (DW_1), most of the second dry season (D_2), and almost the entire second wet season (W_2; Fig. 2). At each census, survivors were measured for their height to topmost alive point of the plant (= relaxed height). Numbers of new leaves produced since, and old leaves retained from, a prior census were also recorded (total = new + prior). Each of these new leaves were also scored on a scale of 1–5 for its missing leaf area (1: <5 %, 2: 5 to <20 %, 3: 20 to <50 %, 4: 50 to <75 %, and 5: ≥75 %). A well-known problem, however, with static measures of herbivory is that they will miss cases of 100 % defoliation or premature leaf abscission, especially of young leaves (Coley and Barone 1996). To track leaf production, pieces of fine copper wire were tied round stems just below points of most recent leaf expansion. Because many big seedlings in flush at census 4 had flaccid leaves, all heights were re-measured to the highest stem point (10–12 November 2009). Stem height regressed on relaxed height had slope values of nearly 1.0 ($\log_{10}(y) = 1.0037 \log_{10}(x) - 0.0011$ and $\log_{10}(y) = 0.9708 \log_{10}(x) + 0.0527$ for *M. bisulcata* and *T. bifoliolata*, respectively; $n = 164$ and 82).

Cages and control rooftops were replaced as soon as possible after any damage to them was noticed. For the faster growing seedlings, cages had to be enlarged, but rarely more than three times, to reach one of the following six sizes: 50 × 50 × 75 or 100 cm, 75 × 75 × 100 or 150 cm, or 100 × 100 × 150 or 200 cm. On an enlargement, the rooftop of the nearest control was also replaced soon afterwards, because the latter was most likely to be in a more similar light environment as the enlarged cage unit. This new mesh material on controls thus ensured that both treatments continued to have similar light transmission, since wearing of mesh slightly reduced this (see ESM resources 3, 4). To maintain sample sizes, those seedlings that had died by censuses 2 and 3 (mostly controls due to felling of their stems near the ground by putative rodents) were replaced, where feasible, by the flagged standbys. These 'replacement seedlings' amounted to 35 *M. bisulcata* (32 for controls) and 3 *T. bifoliolata* seedlings (all controls) added at census 2. Seven more *M. bisulcata* replacement seedlings were added at census 3 (6 controls, 1 caged). This mortality introduced a small but unavoidable confounding effect to our cage treatments, because the latter excluded mammals and not just medium-sized insects as was our original focus. With clipped seedlings discounted, mortality per annum was 7.27 and 3.91 % for control and caged *M. bisulcata*, respectively (likewise for *T. bifoliolata*: 3.97 and 2.51 %).

Data analysis

Growth variables

To standardize for differences in initial plant height (ESM resource 1) 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 were heights at times t_1 and t_2 which corresponded to the start and end of the time interval between censuses (units of cm cm^{-1} $year^{-1}$). The length of time from the median date of census 1 to census 4 was 1.875 year; for intervals DW_1, D_2, and W_2, they were 0.875, 0.333, and

0.666 years, respectively (Fig. 2). Numbers of leaves produced in intervals DW_1, D_2, or W_2 were divided by the corresponding numbers at the start of the census interval, expressed as relative leaf production (of new leaves), RLP-NL (dimensionless).

Using RGR-HT did not bias the analyses in any appreciable way, as has been suggested by Blundell and Peart (2001) that it might under certain conditions. We concluded this on three grounds: (1) the treatment groups (control vs. caged) had near-identical shapes for their frequency distributions and the same ranges of starting heights for each species (ESM resource 2); (2) RGR-HT graphed as a function of starting height yielded a flat relationship, indicating that it was not height-dependent for either species (control group, $P = 0.196$ and $P = 0.476$ for *M. bisulcata* and *T. bifoliolata*, respectively; caged group, $P = 0.134$, $P = 0.467$); and (3) the relationship between absolute growth rate and starting height was also flat (control group, $P = 0.191$, 0331; caged group, $P = 0.112$, 0.397).

Functional responses

To test each species response to herbivory (Fig. 1), and to avoid pseudo-replication, we compared gap-level means of RGR-HT and RLP-NL in each of the intervals DW_1, D_2, and W_2, and their mean final stem height and total number of leaves on seedlings at census 4, between caged and control treatments across the range of light availability measured midway through the experiment (%PPFD-$_{\text{mid}}$). Analyses were repeated for intervals D_2 and W_2 excluding the replaced seedlings. Linear mixed models (LMMs) using REML were run in GenStat v.14.1 (VSNI, Hemel Hempstead, UK) to test for significant differences in slope between caged versus control, i.e. a significant light × treatment interaction term. Gap location was a random (block) term, and explained variation in growth at the between-block level and thus accommodated possible effects arising from spatial autocorrelation across the many gaps. The goodness-of-fit (R^2) of each of the mixed-effects models was calculated using the method of Nakagawa and Schielzeth (2013). Five seedlings had to be omitted in one or more intervals because the caged treatment had been clearly compromised (high defoliation inside the mesh). There were no other signs of breaches of the individually caged seedlings in the gaps by herbivores.

Population matrix models

We built basic 5 × 5 stage-structured models for each of the eight combinations of two species × two treatments × two measures of seedling growth (following Halpern and Underwood 2006: Fig. 1 on p. 925). The stages were seeds, seedlings, saplings, juveniles, and adults. For each species' projected population growth rate (λ), all matrix elements were identical except for the probabilities of a seedling remaining one, and of making the transition to a sapling via growth, i.e. sapling recruitment (P_2 and G_2 respectively). These changed stasis and growth elements were calculated from the impact of herbivory (caged vs. control effect), and depended on whether absolute height growth rate was either represented by the overall median of the surviving seedlings across all gaps or instead by the mean of the upper quartile, Q4 (i.e., the "fast growers"). To calculate G_2, following Zuidema and Boot (2002: p. 10), these annual growth rates were multiplied by the annual probability of seedling survival (S_2) of each species in gaps and then divided by the height difference (cm) between a newly established seedling (see ESM resource 2) and 250-cm-tall stem which is equivalent to a 1-cm dbh sapling (Newbery et al. 2010). In turn, to calculate P_2, this G_2 was subtracted from S_2. Details of other inputs from external data sources required to build the matrices (which assumed no density-dependent dynamics) are provided in ESM resource 6.

Results

Functional responses

In the first interval, DW_1, clear differences were apparent between the functional responses of *M. bisulcata* and *T. bifoliolata*. The impact of herbivores on *M. bisulcata* seedlings increased with increasing light availability (log %$PPFD_{\text{mid}}$) for both RGR-HT and RLP-NL (Fig. 3a, e). This corresponded to a strong impact due to undercompensation, as defined in Fig. 1c. By contrast, slopes for caged versus control *T. bifoliolata* seedlings only marginally diverged for RGR-HT and were not significantly different for RLP-NL (Fig. 4a, e). Nevertheless, caged seedlings outgrew controls in height (main effect of treatment, T). The key to the functional responses depicted in Fig. 1c–f is the significance of the light × treatment interaction term. In the second interval, D_2, with replacement seedlings, the herbivore impact was statistically negligible for both species and both growth variables (Figs. 3b, f, 4b, f). In other words, there was near complete compensation for any damaged tissues in the species (see Fig. 1a). Similar results were obtained for *M. bisulcata* when replacement seedlings were omitted, except that the interaction term for RLP-NL was now significant ($P = 0.024$) (Fig. 1f). Only one *T. bifoliolata* seedling had to be replaced, so analyses were not repeated for this species.

In the third interval, W_2, also with replacement seedlings, the functional response of *M. bisulcata* shifted back towards the pattern in DW_1, showing a strong to

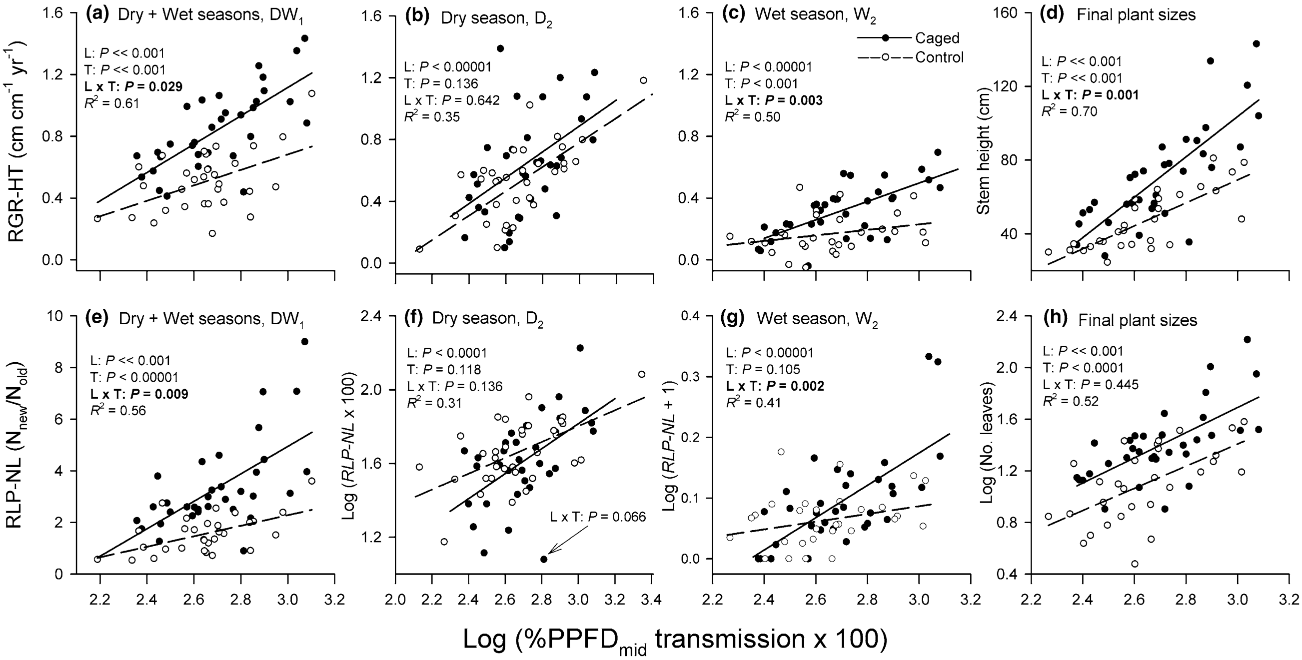

Fig. 3 Growth responses of *Microberlinia bisulcata* to increasing light availability (L) under two herbivore treatments (caged vs. control, T) at Korup, Cameroon. **a**–**c** Relative growth rate in height, RGR-HT, and **e**–**g** the relative production of new leaves, RLP-NL, in three consecutive census intervals, and the **d** absolute heights and **h** number of leaves of seedlings at the end of the experiment. Points represent the individual gap locations, using means of growth and light availability across seedlings data; in **c**, a caged outlier (−0.33 cm cm^{-1} year^{-1}) was removed. The arrow in **f** points to a gap location which, when removed from the sample, markedly changed the probability value of the L × T interaction

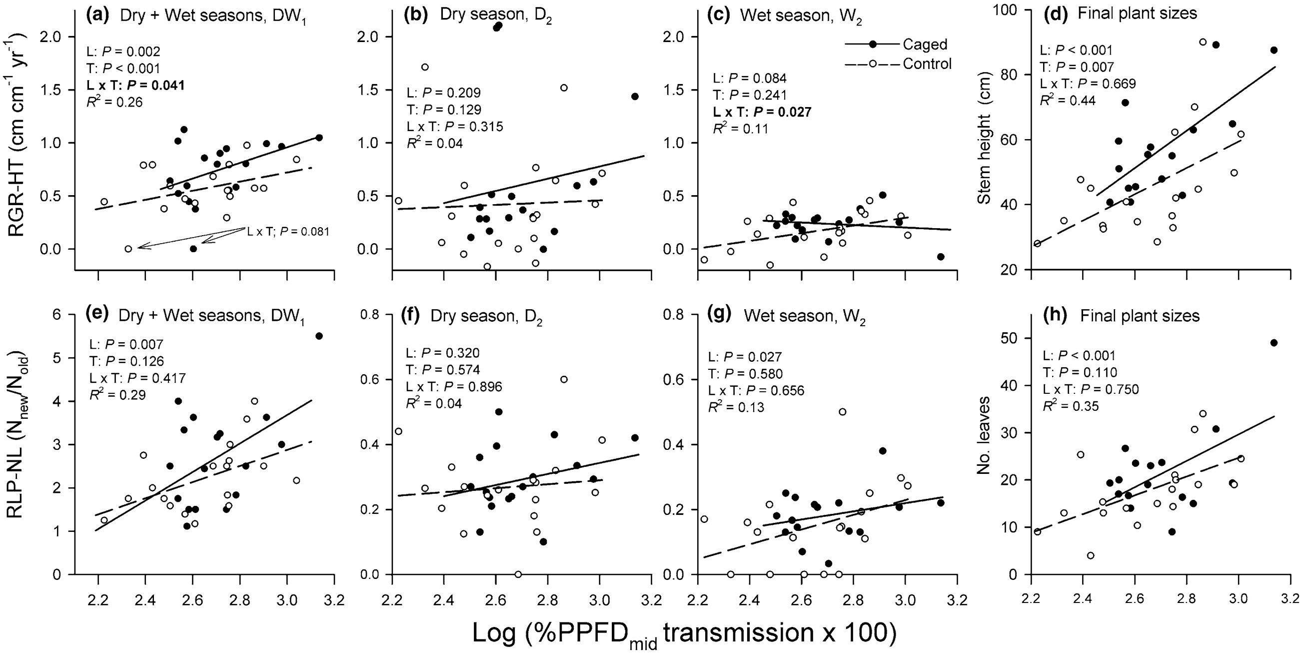

Fig. 4 Growth responses of *Tetraberlinia bifoliolata* to increasing light availability (L) under two herbivore treatments (caged vs. control, T) at Korup, Cameroon. **a**–**c** Relative growth rate in height, RGR-HT, and **e**–**g** the relative production of new leaves, RLP-NL, in three consecutive census intervals, and the **d** absolute heights and **h** number of leaves of seedlings at the end of the experiment. Points represent the individual gap locations, using means of growth and light availability across seedlings data. The pair of arrows in **a** point to an outlying shared gap location which, when removed from the sample, markedly changed the probability value of the L × T interaction

moderate impact. For the controls, RGR-HT was overall much reduced compared to that in DW_1, and seedlings showed very little response to increasing light availability. For caged seedlings though, RGR-HT was likewise lower but responded positively to increasing light availability (Figs. 1h, 3c). For RLP-NL in W_2, there was some evidence of a moderate impact via undercompensation in the upper two-thirds of the range in light levels (Figs. 1f, 3g). With *M. bisulcata* replacement seedlings excluded, this interaction remained significant ($P = 0.027$), but for RGR-HT it did not ($P = 0.382$), reverting to a moderate impact where undercompensation was even across light levels (Fig. 1b). For *T. bifoliolata*, a weak form of overcompensation occurred for RGR-HT (Fig. 1e), but not RLP-NL (Fig. 4c, g).

For *M. bisulcata*, the difference in absolute height at the end of the experiment between control and caged became larger with increasing light availability (Fig. 3d); by contrast, the pattern for *T. bifoliolata* was not significant (Fig. 4d). Although slopes were very similar for the two species under the controls [62.8 vs. 57.6 cm/unit log ($\%\mathrm{PPFD}_{\mathrm{mid}}$), respectively], the slope for *M. bisulcata* when it was caged almost doubled (to 109.5 cm/unit), whereas for *T. bifoliolata* it only increased slightly (Figs 3d, 4d). Leaf numbers showed a moderate impact with even compensation (Fig. 1b) for *M. bisulcata* (Fig. 3h) yet no impact for *T. bifoliolata* (Fig. 4h). These last results confirmed the strong impact of herbivory across the whole experimental period on *M. bisulcata* but little, if any, negative impact on *T. bifoliolata*.

Static percent damage to new leaves produced in each time interval (DW_1, D_2, and W_2) was quite variable among control seedlings, but generally higher in the *M. bisulcata* than the *T. bifoliolata* population (see histograms in ESM resource 7). When species-specific damage was compared on seasonal basis using their median seedling scores, the difference between these two values was lowest in the second dry season, D_2 (= 0.36; median scores of 1.36 for *M. bisulcata*, 1.00 for T. *bifoliolata*), as suggested by their functional responses for D_2 (see Figs. 3b, f, 4b, f). The median damage score for both DW_1 and W_2 was 2.0 (a possible range of 1.0–5.0) for *M. bisulcata*, whereas it was 1.33 and 1.25, respectively, for *T. bifoliolata*.

Population dynamics

With a reduction of herbivores (caged treatment), median estimates of seedling growth rate across all gaps suggest that *M. bisulcata* would require 10.5 years to recruit to a sapling, and *T. bifoliolata* 14.4 years, which are about half and two-thirds the expected recruitment times of seedlings exposed to herbivores (controls, 22.7 and 22.5 years, respectively). Based on these estimates, *M. bisulcata* had a relatively greater increase in population growth rate than *T. bifoliolata* when freed of herbivores (*M. bisulcata*, $\lambda_{\mathrm{control}} = 1.127$ vs. $\lambda_{\mathrm{caged}} = 1.157$; *T. bifoliolata*, $\lambda_{\mathrm{control}} = 1.094$ vs. $\lambda_{\mathrm{caged}} = 1.107$). Considering just the fast-growers (the upper quartile), these being the most likely recruits, the sapling recruitment times were reduced by almost a third for controls, to 8.3 and 7.9 years, respectively, for *T. bifoliolata* ($n = 9$) and *M. bisulcata* ($n = 12$), but only by about half for caged seedlings, to 4.7 and 7.2 years, respectively ($n = 10, 23$). Accordingly, the population growth rate increased for *M. bisulcata* ($\lambda_{\mathrm{control}} = 1.166$ vs. $\lambda_{\mathrm{caged}} = 1.189$) more than for *T. bifoliolata* ($\lambda_{\mathrm{control}} = 1.124$ vs. $\lambda_{\mathrm{caged}} = 1.127$).

Discussion

Our experiment in the P-plot at Korup is novel because we accomplished three things concurrently. First, we physically protected tree seedlings of two locally dominant species from insect attack. Second, we did so in many canopy gaps ($n = 40$) across a large area (c. 80 ha) commensurate with population-wide forest heterogeneity. Thirdly, we tested species' growth responses to herbivory as affected by light on a continuum. Equivalence in ambient light and its transmission through the mesh treatments was verified in detail; such checks are rarely made (see ESM resources 3, 4). The outcome of the study supported our central hypothesis that the early growth and sapling recruitment of *M. bisulcata* is strongly limited by herbivores, and that of the co-dominant *T. bifoliolata* much less so.

One proviso is that the cages also excluded terrestrial vertebrates. But these animals only slightly altered the sample size because they instantly killed some control seedlings of *M. bisulcata*, by completely biting through their stems near the ground (3–11 % across the three intervals, DW1, D2, W2; 0–2.5 % for *T. bifoliolata*). It is for this reason that replacement seedlings for some controls were used where possible. There was no evidence of any other kind of damage—browsing of leaves or shoots, or of seedlings with their tops bitten off or partially uprooted—from vertebrates in this experiment or seen collectively in over 15 years of field work onsite. Therefore, we are quite confident that the impact of vertebrates on *M. bisulcata* seedlings is restricted to mortality via 'stem-clipping'; they did not influence growth rates per se, which shaped the functional responses we investigated (see Fig. 1).

Undercompensation by *M. bisulcata* supports the general prediction of the Plant Vigor Hypothesis (Price 1991; Fig. 1c). Three explanations are possible: (1) with more light, insects preferred larger *M. bisulcata* seedlings that provided them with more food; (2) its leaves were more edible (less resistant) at higher light levels; and/or (3) larger seedlings were more easily found among gap vegetation than smaller ones. By contrast, growth of *T. bifoliolata* was much less impacted by insect herbivores, in spite of it being nearly as vigorous as *M. bisulcata* in the first interval (DW_1), suggesting a general resistance. In support of a causal relationship between herbivory and plant performance is the five-fold and four-fold greater percentage of leaf area damaged in controls than caged seedlings of *M. bisulcata* and *T. bifoliolata*, respectively. Among controls, however, our static measures may have overlooked cases of 100 % defoliations, especially at higher light levels. Although we were unable to systematically sample (diurnally and seasonally) the invertebrates on both tree species' seedlings, grasshoppers, stick insects, and evidence of moth larvae feeding were observed on *M. bisulcata* leaves, though primarily grasshopper nymphs were seen eating *T. bifoliolata*. For neither species was there any sign of damage from shoot-borers.

We hypothesize that *M. bisulcata* is more palatable and nutritious, and less well defended chemically and physically against herbivores, than *T. bifoliolata*. Indeed, preliminary results indicate 43 % higher total phenolics concentrations and 39 % greater leaf mass per area (LMA) in *T. bifoliolata* than *M. bisulcata* leaves. The most plausible argument in favor of this species difference in allocation to constitutive defenses and differential susceptibility to insect herbivores is the Resource Availability Hypothesis (Coley et al. 1985; Endara and Coley 2011). Our results are consistent with its predictions, given the relative difference in the shade tolerance of the two study species and their maximum growth rates; but they cannot be interpreted as a proper test of this hypothesis (which would require at least one more tree species).

In a meta-analysis of plant responses to manipulated herbivory and resource heterogeneity, Hawkes and Sullivan (2001) reported only one woody species tested under changed light conditions (in a greenhouse). Recently, a different meta-analysis of studies involving species' responses to consumer removal and resource addition lacked any woody plants (Viola et al. 2010). In their review of resource effects on plant tolerance to leaf damage, Wise and Abrahamson (2007) documented only three studies that considered light in this context of plant growth: two of which were on grasses and a third on a small tree (*Celtis laevigata:* Ulmaceae) that used three shade levels in a greenhouse (but see also Blundell and Peart 2001; Norghauer et al. 2008; Salgado-Luarte and Gianoli 2010). Although not explicitly tested, a Panamanian study pointed to variable functional responses of three pioneer species when excluded from insects via mesh in 6 small and 11 large artificial gaps (in 12 ha; Pearson et al. 2003). Clearly, to better understand the breadth of functional responses in diverse plant communities to herbivory, forest trees must be included in more experimental field studies.

Our matrix models suggested that insect herbivores, all else being equal, could contribute to curtailing the population growth of *M. bisulcata* (via undercompensation) much more than they could that of *T. bifoliolata*. In their review, Maron and Crone (2006) found that native invertebrate herbivores reduced λ on average by 0.12 in herb and shrub populations; by contrast, λ was reduced by up to c. 0.062 for *M. bisulcata*. Our models, however, considered only dynamics in gaps, which are transient and occupy a small area of the forest at any given time (here c. 6 %; see also Kellner et al. 2009); yet gaps are where seedlings of both species grow best into the sapling stage (>1 cm dbh) (Hartshorn 1978; Denslow 1987). Apart from undercompensation, another important biotic factor also shown to limit the early recruitment of *M. bisulcata* saplings in gaps is vertebrates which eat seeds and cut through seedling stems, thus killing them: their combined impact was estimated to reduce λ by 0.06 (Norghauer and Newbery 2011). Both post-establishment processes combined, over many years, could contribute importantly to the current scarcity of *M. bisulcata* saplings. A stronger impact on the growth of the more competitively dominant species, that is also spatially variable, should in theory help *M. bisulcata* coexist with *T. bifoliolata*, and possibly other tree species in the community as well (Pacala and Crawley 1992).

While both processes suppress *M. bisulcata* seedlings, and probably increase their risk of death following gap closure, re-opening of the canopy nearby, if not too delayed, would allow onward growth (Newbery et al. 2010). Conversely, for the more shade-tolerant *T. bifoliolata,* the near-absence of undercompensation (Fig. 4) should enhance its ability to maintain a much larger bank of stems 1.0–9.99 dbh than *M. bisulcata* (D.M. Newbery, unpublished data); however, this lends only partial support to the notion that dominance of rain forest trees may be promoted by a lack of herbivore impacts on seedlings or saplings (recently reviewed by Peh et al. 2011). Notably, such a role for herbivores was not found for the two African dominants *Gilbertiodendron dewevrei* and *Julbernardia seretii* at Ituri, DRC (Gross et al. 2000). By contrast, Blundell and Peart (2004) found that herbivory increased with seedling abundance for a dominant canopy species, *Shorea quadrinervis*, in a Bornean rain forest.

We have shown that herbivore suppression of *M. bisulcata* seedlings was ameliorated under drier conditions (period D_2 cf. DW_1 and W_2; Fig. 3). In other words, the functional response of this species to herbivory was affected by seasonality. In the tropics herbivory is generally more intense in wetter months, and much less so under drought-like conditions when forest insect abundance is limited physiologically and/or by the quantity and quality of leaves available as food (Coley and Barone 1996; Givnish 1999; Nair 2007; Richards and Coley 2007; Norghauer et al. 2008). Infrequent major drought disturbances are thought to play a determining role in *M. bisulcata* achieving local dominance as groves at Korup (Newbery et al. 2004, 2013), so we would expect an accompanying release from herbivore pressure to enable faster sapling recruitment, not only in gaps, but especially in a better-lit understory across the whole forest.

Conclusions

By manipulating seedling exposure to insects in gaps across a very large area of primary forest, we found that two dominant tree species, *M. bisulcata* and *T. bifoliolata*, showed very different functional responses to herbivory. Our experimental evidence suggests that insect herbivores are playing a key role in limiting the growth and sapling recruitment potential of seedlings of the less shade-tolerant, yet more light-responsive, *M. bisulcata*, but they have a much smaller role in suppressing the more shade-tolerant *T. bifoliolata* population at Korup. Tree-fall gaps are commonly found in many rain forests across the tropics, as are non-pioneer tree species at the lower end of the shade tolerance continuum. Using an explicit framework that integrates these two ecological aspects (Fig. 1) may prove powerful for incorporating herbivory, along with life-history traits, into niche-based models of species coexistence.

Acknowledgments 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 field. All field operations were funded by the University of Bern. The experiments complied with the current laws of the country (Cameroon) in which the experiments were performed.

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