Forest Ecology and Management 310 (2013) 555–566

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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 understory 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.

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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http://dx.doi.org/10.1016/j.foreco.2013.08.029

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 understory, 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 (±SE) annual rainfall has been 5116 ± 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 × 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