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Intraspecific allometries reveal hyper-slender stems in forest gaps and the impact on tree growth from insect herbivores

Julian M. Norghauer[1,2] 🔗

[1]Institute of Plant Sciences, University of Bern, Bern, Switzerland

[2]Statistical Scientific Editing, Montréal, Québec, Canada

Correspondence
Julian M. Norghauer, Institute of Plant Sciences, University of Bern, Altenbergrain 21, Bern, Switzerland.
Email: j.norghauer@videotron.ca, jmnorghauer@zoho.com

Abstract

Conspicuously absent from plant allometric models are insect herbivores, despite their ubiquity in pantropical forests as well as the importance of gauging their impact on plant growth for understanding tree regeneration dynamics. Conceivably, the scaling relationships of plant populations with and without exposure to insects could be compared to gain insight, but this has yet to be tried. Here, I examined the size allometry of three canopy-statured species (Fabaceae) by fitting standard major axis regressions of stem height, number of leaves, and maximum area per leaf against stem diameter (root collar) of their juveniles (seedlings/saplings) in 41 canopy gaps after ca. 2 years of herbivore exclusion (using mesh cages with mesh-rooftop controls), in a central African forest. Herbivores did not change the slope or intercept, nor shift the location of *Tetraberlinia bifoliolata* and *T. korupensis* populations, whose seedlings tolerate shade well. In stark contrast, all three size allometries were altered in the faster-growing *Microberlinia bisulcata*, whose seedlings cannot tolerate shade indefinitely. More pronounced than either an altered slope (scaling exponent) or intercept was the strong rightward shift in location (to larger sizes) of protected *M. bisulcata*, whereas its normal (control) population was left stunted, with fewer and smaller leaves. Nevertheless, all species had higher than theoretically predicted scaling exponents, even in the absence of herbivores, suggesting a convergent response early in tree ontogeny across the shade-tolerance spectrum prioritizing height gain over mechanical stability in forest gaps. But insect herbivores were able to significantly strengthen this deviation in *M. bisulcata*, and perhaps in *T. korupensis*. These results demonstrate an allometric approach may prove useful for revealing how insects differentially impact trees′ growth and form (slenderness) when they are most vulnerable to herbivory.

KEYWORDS
allometry, herbivory, recruitment, saplings, seedlings

1 | INTRODUCTION

Bivariate scaling relationships describe how organismal traits, whether morphological, physiological, or ecological, change with body size (or size of a body part) (LaBarbera, 1989). In plants, this way of quantifying size-dependent differential growth (allometric variability) within populations or across species is perhaps apt for understanding their functional traits and resource allocation patterns in response to biophysical constraints (Kleyer & Minden, 2015; Weiner, Campbell, Pino, & Echarte, 2009) and local environmental conditions (Poorter & Sack, 2012; Weiner, 2004). For trees, how stem height—crucial for intercepting more light and for shading neighbors (asymmetric competition)—changes nonproportionally with stem diameter conferring mechanical strength is of great interest to both ecologists and foresters (Henry & Aarssen, 1999; King, 1996; Kohyama & Hotta, 1990; Muller-Landau et al., 2006; Niklas, 1995; O'brien, Hubbell, Spiro, Condit, & Foster, 1995).

Several prominent theories use an allometric perspective to predict this relationship's scaling exponent (i.e., slope b of log–log scatterplot; Warton, Wright, Falster, & Westoby, 2006). It should take a universal value of 2/3, according to metabolic theory of ecology (West, Brown, & Enquist, 1999) and its subsumed elastic similarity model (McMahon & Kronauer, 1976), but 1/2 for wind-exposed trees under constant stress similarity (Dean & Long, 1986). However, a value of 1 is expected if tree height simply changes in direct proportion to its stem diameter (i.e., isometric scaling) under geometric self-similarity during growth (King & Loucks, 1978). For leaf numbers, whose arrangement and total area determines light capture, both metabolic and geometric models predict $b = 2$ in relation to stem diameter.

Current empirical support for these theories varies from weak to strong (e.g., Alves & Santos, 2002; Coomes, 2006; O'Brien et al., 1995; Osunkoya et al., 2007) and likely depends on whether interspecific or intraspecific allometries are examined (Huang, Lechowicz, Zhou, & Price, 2016), the latter being far less studied (Watt & Kirschbaum, 2011). For example, in many tropical forests, support for metabolic theory is lacking at tree community levels (Muller-Landau et al., 2006), and, because of canopy disturbances, vertical light gradients, and changing light trajectory requirements, its theoretical predictions are unlikely to hold true over the long lifetimes of trees (ontogeny) (King, 1996; Niklas, 1995; Osunkoya et al., 2007; Poorter, Bongers, Sterck, & Woll, 2005). Much of this ambiguity arises because individual neighbors (competitors) and neighborhoods (stand age and density) can influence the height–diameter allometry of trees (Henry & Aarssen, 1999). Despite this

and other criticisms leveled at these invariant scaling theories, notably toward metabolic theory (Coomes, 2006), they are nonetheless useful for gaining insight into *why* departures from idealized ("optimal") architectural patterns might occur (Price et al., 2012). Such variability in tree allometries can provide insight into evolved life-history strategies, in terms of species-specific resource allocation and functional trade-offs, and even climatic and phylogenetic effects (e.g., Hulshof, Swenson, & Weiser, 2015). Within species, examining allometric variation vis-à-vis scaling exponents for populations can reveal to what extent growth, form, and size-related processes critical for trees' recruitment and demographic structuring are influenced by neighbor- and stand-related effects (incl. vines: Dias, dos Santos, dos Santos, & Martins, 2017; or wind loading: Feng, Huang, & Wan, 2019; Thomas, Martin, & Mycroft, 2015).

Herbivores are a ubiquitous biotic factor that nearly all plants must variously tolerate, resist, and escape in seedling stages through adulthood (Bazzaz, Chiariello, Coley, & Pitelka, 1987; Norghauer, Glauser, & Newbery, 2014). Yet interpretations of allometry have generally overlooked their involvement, probably because, in addition to asymmetric competition among trees, derivations of scaling theories ignore herbivory impacts on plant growth and form (Coomes, 2006; Moncrieff, Chamaillé-Jammes, Higgins, O'Hara, & Bond, 2011). Browsing mammals can starkly modify tree architecture by damaging even low amounts of biomass (shoots and buds; Archibald & Bond, 2003; Moncrieff, Chamaillé-Jammes, & Bond, 2014) and their exclusion can strongly shape the allometry of African savanna trees (Moncrieff et al., 2011). In forests, compared with the darker understorey matrix, both seedlings and saplings are prone to greater herbivory by insects in the better-lit openings or "gaps" caused by canopy disturbances (Piper, Altmann, & Lusk, 2018), which could limit their height growth and recruitment rates there (Lemoine, Burkepile, & Parker, 2017; Norghauer, Malcolm, & Zimmerman, 2008; Norghauer & Newbery, 2013). But whether invertebrate herbivores also cause shifts in the scaling of juvenile trees (i.e., seedlings and saplings) remains experimentally untested. If they do, the pertinent question becomes: what could such deviations tell us about how herbivores influence tree growth and form (i.e., slenderness) and recruitment strategies?

Here, I address two basic questions. First, do intraspecific allometric scaling relationships of stem diameter against seedling/sapling height and leaf number/area of canopy tree species follow the predicted scaling exponents from theory? Second, for each species, how does their exposure to insect herbivores in canopy gaps affect key parameters of intraspecific (*static*) size allometries?

2 | MATERIALS AND METHODS

2.1 | Study site

The data came from a 22-month-long herbivore-exclusion experiment conducted in lowland tropical rain forest of Korup National Park, Cameroon, in the 82.5-ha permanent "P-Plot" (established in 1991; Newbery, Songwe, & Chuyong, 1998). The soils here are sandy and nutrient poor, and this forest is among the wettest in the tropics (ca. 5100 mm of rainfall per year, mostly from March through November; Newbery, Chuyong, & Zimmermann, 2006). In the P-plot are groves of three ectomycorrhizal trees: *Micrberlinia bisulcata* A. Chev., *Tetraberlinia bifoliolata* (Harms) Haumann, and *T. korupensis* Weiringa, which co-dominate the canopy as adults; the first is best described as a large, long-lived tree that is light-demanding early in ontogeny, whereas both *Tetraberlinia* congeners attain smaller maximum stem diameters and are much more tolerant of shade as seedlings and saplings (Newbery, Chuyong, Zimmermann, & Praz, 2006; Newbery, van der Burgt, Worbes, & Chuyong, 2013). During masting events every 2–3 years (Newbery et al., 1998), the species produce discoid seeds dispersed ballistically on sunny days in the wet season (Norghauer & Newbery, 2015).

2.2 | Protecting plants from insect herbivores

The field experiment used Econet-B mesh netting (AB Ludwig Svensson, Sweden) to exclude herbivores at 41 blocks (appendix A in the study by Norghauer & Newbery, 2013), each consisting of a canopy gap formation (Figure 1a; paired with an understorey location 35 m [median] away). In each habitat, cages (Figure 1b, background) were built around individual newly established seedlings (Figure 1e–g), with matching controls consisting of a mesh rooftop (sides open; Figure 1b, foreground) accessible to herbivores: both were supported by bamboo posts. Naturally occurring seedlings—similar-aged (2–5 months), all established during the same wet season—were randomized to cages and controls installed over a 1-month period (mid-December 2007 to mid-January 2008). Not all blocks contained all three species, however, due to dispersal limitations: the starting sample had 664 seedlings (heights ranged from 13.5 to 30.30 cm): 388 *M. bisulcata* and 172 *T. biofoliolata* (both species masted in 2007), and 104 *T. Korupensis* (weakly or non-masting population that year). The aim was to prevent caterpillars (Lepidoptera), grasshoppers (Orthoptera), stick insects (Phasmatodea), leaf-cutting bees (Hymenoptera), and other medium-sized or larger insects from damaging the plants' leaves (Figure 1c,d,j); excluding smaller insects (<1–2 mm in width) would require using very fine mesh with two likely confounding ecological effects: too much trapped humidity that favors fungal pathogens and too little light transmission to the newly established seedlings. By using cages, however, mammals were also unavoidably excluded. During the course of the experiment, as seedlings grew taller into saplings, their cages were enlarged accordingly (for each, its nearest conspecific control mesh rooftop as well). The impact of insect herbivores on species-specific growth rates and plant defense syndromes were already reported on, in a trio of papers, where more of the experiment's details (including extensive light and herbivory measurements) can be found (Norghauer et al., 2014; Norghauer & Newbery, 2013, 2015). Because of negligible height growth of all three species in the understorey over ca. 2 years, this study focused on their individuals established in gaps (Figure 1a).

Within these better-illuminated forest areas, the light environment of the caged (final $n = 99$) and control (final $n = 161$) populations was highly similar—not surprisingly, given the randomization used—when measured directly or indirectly above each individual (midway through the experiment, in October/November 2009; appendix B in the study by Norghauer & Newbery, 2013). The *absolute difference* between them in their mean, median values for percent canopy openness was almost nil, at 0.01%, 0.09% (from hemispherical photography; one missing cage value [i.e., $n = 160$]), and likewise differing by just 0.02%, 0.14% for the incident percentage of above-canopy light photosynthetic photon flux density (PPFD) under overcast conditions.

2.3 | Plant size measurements

At the end of the treatment period (mesh material removed, bamboo posts left in the ground), I counted the standing *number of leaves* (fully expanded, greened) per surviving experimental plant in the 41 gaps (on October 4–9, 2009). About a month later, *stem height* was measured perpendicular to the ground to highest (non-leafy) part of each (on November 10/11, 2009), to the nearest 0.5 cm (because of the sandy soil). In the interim, some individuals ($n = 9$, of which 8 were *M. bisulcata*) had been clipped at their base (Table S1), presumably by rodents—these animals had also reduced the number of *M. bisulcata* controls available during the experiment—so they could not be used for this size allometry analysis. Next, *neighboring vegetation* around each seedling was assessed systematically (also described in appendix E in

FIGURE 1 A recently formed canopy gap created by a fallen tree (windthrow) in a central African rain forest (Korup National Park, Cameroon) (a). The newly established seedlings and later saplings of three codominant trees experimentally studied for herbivore effects on their allometric growth: *Microberlinia bisulcata* (e, h), *Tetraberlinia bifoliolata* (f, i), and *T. korupensis* (g, j), whose exposure to leaf damage (d) from medium-sized insect herbivores, such as grasshoppers (c) (but also caterpillars, and perhaps stick insects; not shown) was prevented by the mesh-lined cages (b, background), or not (b, foreground). The red arrows point to a second POM (point-of-measurement) taken along the plant stem, where the cotyledons had emerged (*cotyledon scar diameter*, *CSR*). In (h), the blue arrows indicate the young, recently expanded leaves of *M. bisulcata* highly susceptible to herbivory from insects; the yellow arrow points to the sapling's main stem. Plagiotropic branching (monopodial and sympodial) characterize all three species; *M. bisulcata* and *T. korupensis* have pinnate leaves, whereas *T. bifoliolata* leaves are compound (f, i), having two lobed leaflets (each counted as a leaf). Photo credits: J. M. Norghauer [Color figure can be viewed at wileyonlinelibrary.com]

the study of Norghauer & Newbery, 2013). Briefly, at each seedling/sapling location, a quadrat delineated by the four bamboo posts was established—hence its area was not fixed, since taller individuals had larger cages and control rooftops than did shorter ones—was estimated over which I visualized a 3 × 3 grid at two height

strata; for each, occupancy of green leafy material in half-squares were counted out of 36 (i.e., 18 full squares per strata); also counted were the number of heterospecific woody stems taller >50 cm growing in each quadrat. About 1–2 weeks before (on October 27 to November 4, 2009), the stem diameter of each individual was measured in two places: at the plant base (ground soil surface, litter removed) corresponding to the *root collar diameter* (RCD), and again, higher along the stem, using as a point-of-measurement (POM) where the cotyledons were shed (hereon, *cotyledon scar diameter*, CSD) (Figure 1e–g). Presumably, the CSD can be measured more accurately and easily than the RCD that is more irregular in shape, or often submerged in soil. Further, since the hypocotyl length varies negligibly with seed size (mass) (in *Brassica campestris*: Pandya, Khan, Gupta, & Dhindsa, 1973; in *Pinus sylversis* [Scots pine]: Castro, 1999), it would imply that, at least for intraspecific allometric constructions, the CSD could be robust to differences in seed size variation within populations. This might be why, for their study of root and shoot allometry of a conifer tree, Rose and Haase (2005) measured stem diameters just below the cotyledon scar on the seedlings (< 1 year old). So, at each stem position, two orthogonal measurements of diameter were taken (mean used), with dial calipers (nearest 0.1 mm). Meanwhile, *maximum area per leaf* was also determined per individual plant as the mean of 3–5 of its apparently largest leaves, for which L × W measurements were taken to obtain leaf area (in cm^2) based on species-specific regressions (detailed in the study by Norghauer et al., 2014).

2.4 | Data analysis

For the allometry analysis, for each species (i.e., intraspecifically), its scaling of stem height, number of leaves, and max. leaf area as a function of RCD was quantified for control and caged populations by line-fitting. Standardized major axis (SMA) regression was used (Warton et al., 2006) to test for common slopes and elevations (*y*-intercepts), as well as expected shifts in location along the *x*-axis, between the control and caged lines. The SMA's strength lies in minimizing the residuals in both the *y* and *x* variables, and not the *y* alone as done in ordinary least squares regression (Model I type). Following Warton et al. (2006), to test for differences in SMA-fitted slopes, a likelihood ratio test statistic was used and compared to a chi-square distribution; to test for differences in elevation or shift, the recommended Wald statistic was used (each test had 1 d.f.). Bootstrapping generated 95% confidence intervals for a line's slope and intercept parameters (200 resamplings).

All size variables were initially log$_{10}$ transformed (with 1 added to *number of leaves*). But in checking the log transformations made, it was clear that max. leaf area was not linearly related to RCD for two species (Figure S1); however, linearity was approximately maintained when plotting nontransformed max. leaf area against log-transformed RCD, so this was instead used. Beyond the nine SMA regressions (i.e., 3 species × 3 scaling relationships) done with RCD, the allometry analysis was repeated using CSD as the *x*-axis variable. All analyses were implemented in GenStat v16.0 (VPN International, Rothamsted, UK).

3 | RESULTS

For the SMAs using RCD, the estimated parameters and corresponding statistics (slope, 95% confidence interval [95%$_{CI}$]) are in Table 1 (those using CSD on the *x*-axis can be found in Table S2). For stem height, all scaling exponents (= slope, or "allometric coefficient") exceeded theoretically predicted values of 2/3; whether exposed to herbivores or not, none of their 95%$_{CI}$ overlapped with 2/3 (and therefore not 1/2 either). Similarly, for all three species, the scaling exponents exceeded 1 in the presence of herbivores (i.e., control group), and their 95%$_{CI}$ did not include it. Lacking herbivores, its height–RCD relationship was still not isometric for either *M. bisulcata* or *T. korupensis* but could be for *T. bifoliolata* (lower bound of 95%$_{CI}$ = 0.92).

For number of leaves, the expected scaling exponent of 2 was very closely met by *T. korupensis*, irrespective of herbivory (Figure 2f). For *M. bisulcata* under normal growing conditions (control group), this value fell just within its 95%$_{CI}$, but not so when protected from herbivores. In contrast, as Figure 2(e) shows, this scaling exponent for leaf number was far lower in *T. bifoliolata*, though its 95%$_{CI}$ did include 2 (Table 1).

For *M. bisulcata*, its exposure to herbivores in gaps altered its height–RCD allometry considerably, increasing its scaling exponent by 24% compared with the caged group (likelihood ratio = 8.45), with a stronger effect (30% increase) on its number of leaves (likelihood ratio = 7.46; Figure S2; Figure 2, Table 1). In contrast, the corresponding exponents for both *Tetraberlinia* species were negligibly affected by herbivores, especially so with respect to leaf numbers (all *p*-values > 0.11; Table 1). However, for *T. bifoliolata*, there was some evidence that herbivores could have elevated the intercept of the fitted height–RCD relationship (Wald statistic = 3.48).

For the max. leaf area–RCD relationship, protection from herbivores negligibly affected its scaling exponent for all three species (*p*-values > 0.25; Table 1) and their

TABLE 1 Parameter estimates and statistics for allometric scaling relationships of plant size traits relevant for light capture (*Y*-variable) against stem diameter (RCD: root collar diameter) for three tree species, protected from insect herbivores (caged) or not (control), in canopy gaps, in a central African rain forest (Korup National Park, Cameroon). Standard major axis (SMA) linear regressions were fitted to the log-transformed variables (except "Max. leaf area"). 95% CI: 95% confidence intervals generated by bootstrapping each sample of data (200 resamplings)

Y-variable	Species	Group	*n*	R^2	Slope	95% CI	*p-value* [slope]	Intercept	*p-value* [intercept]	Shift in location?
Stem height	*Mb*	Control	41	0.86	1.39	1.28–1.62	**0.004**	0.67	0.254	**Yes***
		Caged	94	0.85	1.12	1.03–1.24		0.88		
	Tb	Control	37	0.77	1.43	1.22–1.72	0.136	0.65	**0.062**	No
		Caged	40	0.74	1.20	0.92–1.49		0.85		
	Tk	Control	21	0.75	1.60	1.35–1.99	0.117	0.52	0.871	No
		Caged	27	0.74	1.25	1.04–1.63		0.77		
No. of leaves	*Mb*	Control	41	0.76	2.38	2.04–2.89	**0.006**	−0.54	0.365	**Yes***
		Caged	94	0.78	1.83	1.62–2.00		−0.12		
	Tb	Control	37	0.56	1.75	1.36–2.27	0.497	0.25	0.835	No
		Caged	40	0.55	1.57	1.09–2.24		0.17		
	Tk	Control	21	0.66	2.06	1.68–2.51	0.966	−0.27	0.446	No
		Caged	27	0.70	2.07	1.49–2.74		−0.31		
Max. leaf area	*Mb*	Control	38	0.78	86.2	75.3–95.7	0.610	−36.7	**0.017**	**Yes***
		Caged	89	0.71	90.6	77.4–105		−36.7		
	Tb	Control	36	0.71	98.9	80.9–116	0.253	−45.0	0.892	No
		Caged	39	0.39	82.3	61.3–123		−32.9		
	Tk	Control	20	0.65	140.0	108–172	0.656	−59.7	0.960	No
		Caged	24	0.66	152.2	94.0–207		−68.7		

Note: Results of notable herbivore impacts are in bold.

Abbreviations: Mb, *Microberlinia bisulcata*; Tb, *Tetraberlinia bifoliolata*; Tk, *T. korupensis*.

*$p < .001$.

intercepts for both *Tetraberlinia* congeners (Figure 2h,i). For *M. bisulcata*, however, exposure to herbivores lowered its intercept by 10% (Wald statistic = 4.87; Table 1; Figure 2g), indicating proportionally larger leaves were produced when freed of herbivores than in controls, across all stem diameter sizes.

Crucially, only for *M. bisulcata* were marked shifts in location found, for all three size allometries investigated (Wald statistic = 23.4–29.9; Table 1, Figure 2a,d,g). Hardly any control plants survived to become larger than ca. 8-mm in stem diameter. This species-specific location shift agreed well with the mean (±*SE*) values of stem height, diameter (RCD), and number of leaves of *M. bisulcata*, which were considerably (33%) lower with versus without herbivores, being 48.1 ± 3.7 cm versus 72.0 ± 3.6 cm, 5.3 ± 0.3 mm versus 7.4 ± 0.4 mm, and 16 ± 2 versus 34 ± 5, respectively. In contrast, the corresponding sizes for *T. bifoliolata* were far less different, being 48.4 ± 3.5 cm versus 56.4 ± 3.7 cm, 5.2 ± 0.3 mm versus 5.5 ± 0.3 mm, and 19 ± 2 versus 21 ± 1, these closely matching those of its congener, *T. korupensis*, at 48.8 ± 4.0 cm versus 53.6 ± 3.6 cm,
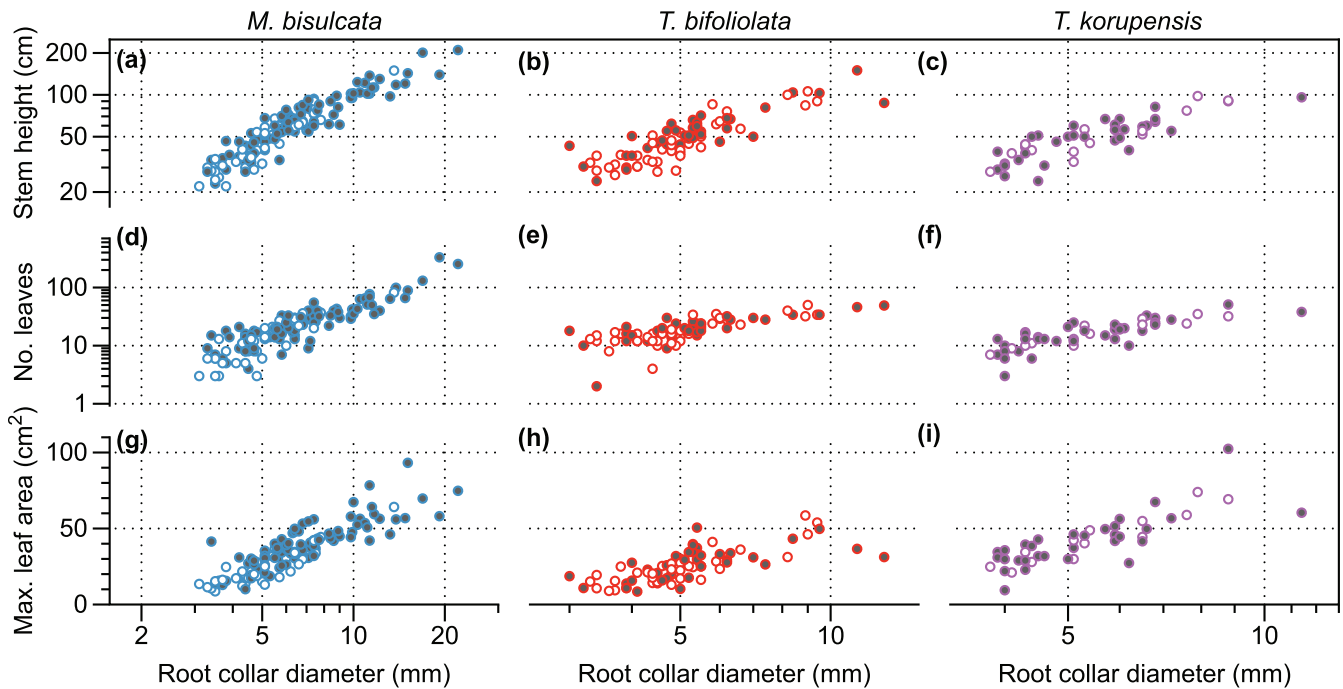
FIGURE 2 Three plant size traits plotted against stem diameter (measured at the ground soil surface) of *Microberlinia bisulcata*, *Tetraberlinia bifoliolata*, and *T. korupensis* individuals growing in canopy gaps in a central African rain forest. The open and filled circles are individual tree seedlings/saplings with and without insect herbivores accessible to them, respectively. Refer to Table 1 for sample sizes [Color figure can be viewed at wileyonlinelibrary.com]

5.3 ± 0.3 mm versus 5.8 ± 0.3 mm, and 17 ± 2 versus 19 ± 2. (For the sample sizes, refer to Table 1.)

For each tree species, the neighboring vegetation of experimental individuals was similar between those with and without herbivores (Figure 3). This was the case whether assessed using coverage that included taller woody stems (Figure 3a; Wilcoxon–Mann–Whitney tests: U = 216–1901, *p*-values = 0.163–0.903) or coverage consisting only of green, leafy vegetation (Figure 3b; U = 216–1920, *p*-values = 0.163–0.975). This suggested each species' control and caged populations experienced similar levels of competition for light and space, but unknown effects may have arisen beyond the immediate vicinity of juveniles, notably belowground.

Compared with RCD, using CSD as the stem diameter POM in the above size trait relationships generally gave similar results. The sole exception was the height–RCD allometry of *T. korupensis*: this scaling exponent was now increased by 33% under exposure to herbivores (likelihood ratio = 4.27, *p* = 0.039, Table S2). Generally, for all three species, slightly better goodness-of-fits (i.e., higher R^2 values) were obtained for 89% of the SMA regressions (16 of 18), when using CSD instead of RCD in constructing their allometries.

Finally, empirical scoring of damage to new leaves confirmed the mesh cages generally prevented insect folivory. All species' caged populations had highly skewed

distributions of percent damage (per plant), with medians of 1% in all three censuses made (except 2.9% for *M. bisulcata* at the end of the second wet season; Figure S3). Within species, these caged medians were 5–15 times lower than the controls in *M. bisulcata*, but at most four times lower in *T. bifoliolata* (one-tailed Wilcoxon–Mann–Whitney tests, U-values: 241–956, all *p*-values ≤ 0.001), while for *T. korupensis*, in part because of the smaller samples sizes, these treatment differences were less pronounced (U-values: 171, 184, 127, corresponding *p*-values of 0.015, 0.013, and 0.126). Among the species' controls—that is, under normal growing conditions—*M. bisulcata* incurred up to 4 and 11 times more damage than did *T. bifoliolata* and *T. korupensis*, respectively (Kruskal–Wallis tests per census, d.f. = 2, H-values: 38.7, 8.1, 6.4, *p* < 0.001, *p* = 0.017, *p* = 0.040; Figure S3).

4 | DISCUSSION

In this article, the *static allometry* of several plant size traits was examined for populations of small trees of similar known age (ca. 24–27 months old), with and without exposure to insect herbivory, in a central African lowland forest. Surprisingly, the only other study I could find, of how herbivores might modify trees' height–diameter allometry via animal exclusions in the field, was done in an African
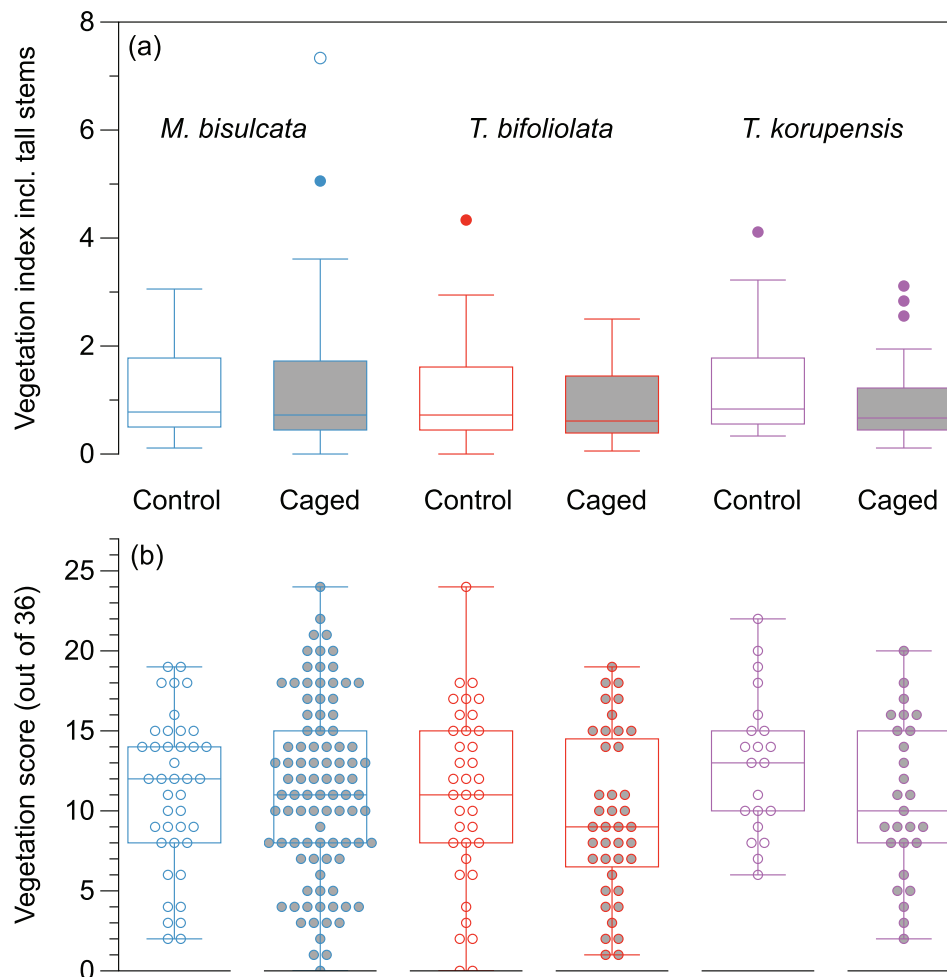
FIGURE 3 Neighboring live vegetation surrounding each experimental plant individual used in the herbivore exclusion field experiment. Each symbol is the location of a surviving seedling/sapling of *Microberlinia bisulcata*, *Tetraberlinia bifoliolata*, and *T. korupensis*, which had been either unprotected (control) or protected (caged) from insects in canopy gaps in a central African rain forest. In (b), the scores are leafy vegetation present in half-squares summed over two strata (≤50 cm and >50 cm); each stratum consisted of 9 squares (× 2 strata = 18 squares surveyed per location). Open and closed (gray-filled) circles are control and caged individuals, respectively. In (a), to account for possible asymmetric competition from woody stems (non-leafy) neighbors >50-cm tall, those scores shown in (b) were divided by 9 (therefore, scaled to out of 4) to which stem counts were added; here, the closed (blue-filled) circles shown are outliers (1.5 times beyond the IQR [inner quartile range]) while the lone open circle denotes an extreme outlier (3 times beyond the IQR). Both vegetation variables served as limited proxies for potential plant competition [Color figure can be viewed at wileyonlinelibrary.com]

savanna system where mega-herbivores (giraffes, elephants) strongly suppressed *Acacia nigrescens* and *Colophospermum mopane* (Moncrieff et al., 2011). So, there is ample opportunity for ecologists and foresters to explore plant–herbivore interactions from an allometric perspective to gain further insights into their relevance for trees' functional ecology, life history strategies, and population dynamics.

4.1 | Herbivore impacts on seedlings and saplings in forests

Despite being very small animals, insect herbivores were able to subtly influence the height–diameter allometry of

M. bisulcata growing in forest gaps (canopy openings). Although counterintuitive, slope values (scaling exponents) were *lower* in the absence of herbivores for both the height and leaf numbers—that is, growing relatively more in height (not in absolute terms) per unit change in stem diameter than when caged (Figure S2, Table 1)— suggesting a coordinated, compensatory response to herbivory, consistent with an attempt at its *tolerance*. This agrees well with prior work showing that, among the three codominant species at Korup, *M. bisulcata*'s leaves are the most nutrient rich and least resistant against insect herbivores, in having the lowest leaf mass per area (LMA) and phenolic content, yet it can best tolerate defoliation in forest gaps in terms of height growth after being

experimentally defoliated (Norghauer et al., 2014). Unlike vertebrate animals that can starkly modify trees' allometry, and hence architecture, because they repeatedly browse shoot tips (Archibald & Bond, 2003; Moncrieff et al., 2011, 2014), leaf-chewing insects adversely impact plants by removing only portions of photosynthetic area (no shoot-boring insects attack *M. bisulcata*). In this respect, *M. bisulcata* was evidently and consistently under greater herbivory (least so in the dry season, as expected), with individual levels of leaf damage exceeding 60%, which rarely happened in either *Tetraberlinia* species. So, incurring this type of herbivory, *M. bisulcata* then flushes a new set of leaves (Figure 1h), albeit proportionally smaller in area across all stem diameters (Figure 2g, Table 1), a process necessarily entailing some plant height increment (Norghauer et al., 2014). This result also implies that *M. bisulcata* is capable of considerable plasticity when growing in canopy gaps. Intriguingly, using the CSD as the POM revealed that *T. korupensis* might likewise engage in a tolerance response, given the significantly higher scaling exponent of its control (1.61) than caged (1.21) populations (Table S2). A possible explanation for this interspecifically congruent response to insect herbivory might lie within the similar pinnate leaf morphology of the two species (Figure 1).

But these partly eaten individuals cannot engage in this compensatory growth indefinitely because gap-filling and diminishing light resources; hence, the lack of larger-sized individuals in the latter half of the diameter range (Figure 2a,d,g) and the strong, rightward shifts in location of all three size allometries of *M. bisulcata* (Table 1). This modification of allometry eclipsed the comparatively minor difference in slopes discussed above and corroborated the strong negative effects of insect herbivores on relative growth rates (height, same leaf characteristics) of *M. bisulcata*, but not the slower-growing *Tetraberlinia* species, previously reported by Newbery et al. (2013). This robust correspondence between allometries and growth rates may derive, in part, from having studied the dynamics of a similar-aged cohort of natural, newly established seedlings. Future work evaluating herbivory impacts on tree regeneration via scaling relationships should nonetheless consider possible plant age effects upon it.

4.2 | Allometry for plant–herbivore interactions and tree regeneration dynamics

To assess herbivory's impact on plants when excluding herbivores, one may examine histograms of their individual sizes or their biomass in terms of ratios (shoot: root especially), or gain stronger inference of demographic consequences by directly measuring plant dynamics (changes in size and survivorship over time). But another way is the allometric approach, as demonstrated here for insects. This could be practically valuable in forests, tropical and temperate to readily gauge the impact of herbivory on trees' form and functioning (e.g., Pittermann, Lance, Poster, Baer, & Fox, 2014) and performance (growth, mortality, recruitment rates), either at the individual or stand level, especially of faster growing, light-demanding timber species that are long-lived such as *M. bisulcata* in addition to some Meliaceae trees (e.g., *Swietenia macrophylla*; Norghauer et al., 2008). Doing so may yield insight into the ecology and regeneration dynamics of populations and communities, and perhaps let us make better use of allometry parameters when modeling herbivore impacts more widely.

4.3 | Universal scaling: Relevance to tree regeneration in gaps?

But whether protected or not from herbivory, empirical scaling exponents of stem height–diameter allometry (range: 1.12–1.60; Table 1) of forest seedling/saplings exceeded the predicted 2/3 or 1/2 of the metabolic/elastic similarity and constant stress models, respectively. Canopy gaps are competitive environments for newly established tropical trees (Denslow, 1987), for which, as suggested by Muller-Landau et al. (2006), the scaling exponent predicted by metabolic theory would probably not be met. Likewise, wind is a natural disturbance that drives gap formations (Mitchell, 2012) and it was shown to increase the stem taper of 1-year-old *Populus* saplings (Feng et al., 2019), but tropical forest seedlings and saplings are likely less exposed to wind-induced mechanical stress, even in gap areas, being closer to the ground and shielded by the surrounding taller trees and dense vegetation. Earlier, Niklas (1995) had suggested geometric scaling should prevail early in plant development (supported by examples of temperate trees). But this, too, clearly did not apply at Korup, where under normal conditions (viz. growing with herbivores) all three tropical species I studied did not maintain a constant proportionate size, showing instead convergent "hyperallometric" relationships between height and diameter early in ontogeny when light was less limited. Interestingly, they also converged closer to isometry in the absence of herbivores, consistent with geometric growth being an idealized process. Thus, intraspecific size allometry of seedlings and saplings appears strongly shaped by phenotypic plasticity in response to locally changed environmental conditions.

Higher scaling exponents for juvenile tree heights (i.e., becoming more slender) may be generally expected where competition for light is intense and asymmetric (Bohlman & O'Brien, 2006; Coomes, Lines, & Allen, 2011; Osunkoya et al., 2007). Becoming taller by sacrificing some mechanical stability would increase woody plants' fitness more than gains in whole-body biomass per se (Moncrieff et al., 2014), by enabling them to position new leaves higher from the ground, in better-lit conditions and above nearby competitors (Kohyama & Hotta, 1990; Poorter et al., 2005). Similarly, using ground-level diameters, higher-than-predicted (>1) slopes were also found in unbranched saplings of the pioneer *Rhus trichocarpa* in secondary temperate forest (Osada, 2005); in juveniles of the fast-growing Fabaceae tropical tree, *Schizolobium parahyba* (Sampaio-e-Silva, Tiberio, Dodonov, & Silva Matos, 2015); in four of seven woody species in cerrado (Dodonov, Lucena, Leite, & Silva Matos, 2011), as well as juvenile palms of *Euterpe edulis* (but not *E. oleracae*) in the Atlantic rainforest (Tiberio, Sampaio-e-Silva, Dodonov, Garcia, & Silva Matos, 2012); but not for saplings of 12 species in gaps of Amazon *cattinga* forest whose POM was taken at a 0.5-m-stem height (pooled slope = 0.73; Coomes & Grubb, 1998). That the three Korup tree species all became more slender to the same degree (Table 1: overlapping 95%$_{CI}$ of control populations), despite pronounced differences in their shade-tolerance traits, is consistent with the finding of increases in LMA and leaf nitrogen being similar among eight tree species varying in branching form (lateral vs. vertical-growth) and successional status in response to canopy openings in a temperate forest (Takahashi, Seino, & Kohyama, 2005), and likewise for the changed LMA among African tree species' (nonpioneer subset) seedling responses to higher irradiance (Veenendaal et al., 1996). But herbivores exacerbated the divergence from predicted slopes, clearly making *M. bisulcata* stems more slender, as well as *T. korupensis* but to a lesser extent (when using the CSD as POM, Table S2), with the form of *T. bifoliolata* the least influenced (Table 1). Yet for leaf numbers, the above reasoning does not hold, as the Korup species' scaling exponents were mostly around 2, in this respect supporting the metabolic and geometric models.

4.4 | Shifts in height–diameter allometry: Attenuating light availability and ontogeny

But in all forests, temperate or tropical, the gaps eventually close up with lateral and upward infilling of vegetation. The corollary is the height scaling exponent should decline

under more light-limiting conditions. Indeed, it does for *M. bisulcata* (Figure 4; no data available for *Tetreberlinia* spp.), to about 3/4, irrespective of the POM used and this "hypoallometry" indicates suppressed height growth. Yet these values still exceed the theoretical 2/3 (no overlap with 95%$_{CI}$ of either slope), likely because metabolic/elastic similarity models harbor overly simplistic assumptions and ignore plant competition and disturbance agents (Coomes, 2006; Moncrieff et al., 2011; Watt & Kirschbaum, 2011), and are similar to the 0.74 reported for *Prioria copaiferia*, a fast-growing canopy-emergent Fabaceae tree that can form dense stands in Panama, for which the 2/3 did not hold either (O'brien et al., 1995). This is perhaps not coincidental and may point to
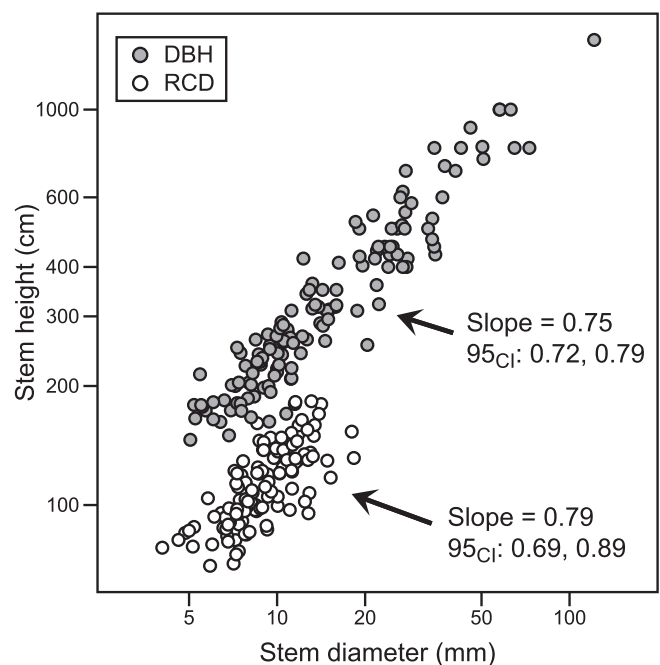
FIGURE 4 Height–diameter relationships for juvenile *Microberlinia bisulcata* trees in the rain forest of Korup National Park, Cameroon. The sample consisted of 124 "seedlings" (i.e., < 75-cm tall), for which root collar diameter (RCD) served as stem diameter, and 135 "saplings" (individuals at least 75 cm tall) for which stem diameter at breast height (DBH; 1.3 m) was used. Most plants were in understorey conditions (three stump-like individuals [main stem clearly snapped before] were excluded). Despite a differing POM (point-of-measurement), slope values were similar for standard major axis regressions of log-transformed heights and diameters ($p = 0.491$), but their intercepts clearly differed (Wald statistic = 930.5, $p < 0.001$). All measurements were made in April 2009, except for $n = 30$ taken on July 30/31 and August 1, 2009; these juveniles had been searched for within 20 1-ha blocks distributed across the 82.5 ha of the P-plot, as part of a study of this tree's density-dependent dynamics (Norghauer & Newbery 2016). This set of size measurements was not used in that paper's analyses (and it includes an additional four half-blocks of forest searched)

phylogenetic effects arising from shared functional traits among very light-responsive albeit long-lived species; it also supports the view that sapling architecture changes with trees' ontogeny (Alves & Santos, 2002; Poorter et al., 2005). Further, the diminished scaling exponent from gap to understorey environments is consistent with the regeneration strategy of *M. bisulcata* capitalizing on multiple gap events to quickly grow upwards (Newbery, Praz, van der Burgt, Norghauer, & Chuyong, 2010) vis-à-vis the two *Tetraberlinia* spp., whose more shade-tolerant seedlings and saplings are common at Korup (Newbery et al., 1998; Newbery, Chuyong, Zimmermann, & Praz, 2006). An interesting idea is whether the high plasticity of *M. bisulcata* would enable its allometry to markedly change so it attains greater heights for a given diameter under the successive, regional drought disturbances thought to promote its adult recruitment and grove formation (Newbery et al., 2013).

4.5 | Where to measure stem diameter on tree seedlings and saplings?

Using CSD for stem diameter gave near identical results to RCD in the allometry analysis for the three species, whether or not herbivores were excluded. These results suggest that, *for tree species whose cotyledons are raised aboveground* during seedling establishment, the CSD may offer another, easier to access POM for use in future allometric investigations of regenerating tree populations before they attain the typical 1.3 m height for DBH (diameter at breast height). This possibility is highly relevant to the tropics, where this epigeal germination trait characterizes the majority of flora in tropical forests (ca. 65% of species; figure 3.2 in the study by Garwood, 1996). I am unaware of any other allometry study of tropical species that has used stem diameter where the cotyledons once were, but it was relied upon in a temperate study of outplanted Douglas-fir seedlings (<1 year old, *Pseudotsuga menziesii*; Rose & Haase, 2005). Of course, the CSD precludes hypogeal species (cotyledons remain belowground) and is likely not useful for individuals with damaged stems or sprouting multiple stems near the ground surface. Whether CSD can be used with interspecific data of seedlings/saplings in allometric models is uncertain, but it is worth investigating, theoretically and empirically. Naturally, once woody stems are tall and wide enough to measure their DBH (typically at a 1-cm threshold), this POM is preferable; partly because it becomes harder to locate the cotyledon scar (unless it was marked earlier) later in ontogeny, but more so to facilitate standardized comparisons of larger saplings and juveniles among tree species and forest sites.

5 | CONCLUSION

By physically excluding them, how insect herbivores may adversely affect the growth of tree seedlings and saplings can be readily inferred from location shifts in their static size allometry, as well as changed scaling exponents (for height, leaf number) and intercept (for leaf area against stem diameter). However, unlike leaf numbers, the intra-specific height–diameter relationship does not follow universal scaling predictions, likely because of the plant fitness premium placed on accruing height and avoiding asymmetric competition when light is provisionally most available (i.e., in forest gaps), a deviation that can be exacerbated by herbivory. Since canopy-statured species evidently experience a range of light environments and herbivores before their juveniles attain maturity, it is unlikely a single scaling exponent always applies throughout ontogeny. Instead, it may be more prudent to focus less on species and more on individual variation in populations when trying to distinguish functional or phylogenetic syndromes in forest tree allometries.

CONFLICT OF INTEREST
None to declare.

ORCID
Julian M. Norghauer https://orcid.org/0000-0002-6484-6879

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