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Canopy gaps promote selective stem-cutting by small mammals of two dominant tree species in an African lowland forest: the importance of seedling chemistry

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Abstract: Small mammals can impede tree regeneration by injuring seedlings and saplings in several ways. One fatal way is by severing their stems, but apparently this type of predation is not well-studied in tropical rain forest. Here, we report on the incidence of 'stem-cutting' to new, wild seedlings of two locally dominant, canopy tree species monitored in 40 paired forest understorey and gap-habitat areas in Korup, Cameroon following a 2007 masting event. In gap areas, which are required for the upward growth and sapling recruitment of both species, 137 seedlings of the long-lived, light-demanding, fast-growing large tropical tree (*Microberlinia bisulcata*) were highly susceptible to stem-cutting (83% of deaths) — it killed 39% of all seedlings over a *c.* 2-y period. In stark contrast, seedlings of the more shade-tolerant, slower-growing tree species (*Tetraberlinia bifoliolata*) were hardly attacked (4.3%). In the understorey, however, stem-cutting was virtually absent. Across the gap areas, the incidence of stem-cutting of *M. bisulcata* seedlings showed significant spatial variation that could not be explained significantly by either canopy openness or Janzen–Connell type effects (proximity and basal area of conspecific adult trees). To examine physical and chemical traits that might explain the species difference to being cut, bark and wood tissues were collected from a separate sample of seedlings in gaps (i.e. not monitored for stem-cutting). These analyses suggested that, compared with *T. bifoliolata*, the lower stem density, higher Mg and K and fatty acid concentrations in bark, and fewer phenolic and terpene compounds in *M. bisulcata* seedlings made them more palatable and attractive to small-mammal predators, likely rodents. We conclude that selective stem-cutting is a potent countervailing force to the current local canopy dominance of the grove-forming *M. bisulcata* by limiting the recruitment and abundance of its saplings. Given the ubiquity of gaps and ground-dwelling rodents in pantropical forests, it would be surprising if this form of lethal browsing was restricted to Korup.

Key Words: Africa, canopy disturbance, plant recruitment, plant resistance traits, regeneration, seedling predation, small mammals, tree phytochemistry, tropical forest

INTRODUCTION

Because terrestrial small mammals are formidable predators and dispersers of seeds they may have important consequences for plant populations, secondary succession, and species composition and coexistence (Crawley 1983, Janzen 1970, 1971; Harper 1977, Maron & Crone 2006, Vander Wall 2010). Unlike for seeds, however, far fewer studies have investigated post-establishment seedling mortality from small mammals (Alvarez-Clare & Kitajima 2009, Osunkoya *et al.* 1993, Paine & Beck 2007, Sork 1987, Theimer *et al.* 2011), especially in forests of equatorial Africa (Clark *et al.* 2012, Hall 2008, Norghauer & Newbery 2011, Struhsaker 1997) where more mammalian biomass is ground-dwelling than in the Neotropics (Malcolm 2004).

Of the small mammals, the rodents (Rodentia), have continuously growing incisor teeth that must be worn down by gnawing. Long ago, Watt (1919) thought this was why 18% of British oak seedlings and saplings had their stems severed or 'cut off' by mice, although beech stems were less susceptible (Watt 1923). That gnawing of seedlings by voles and mice differs starkly among temperate tree species is now appreciated (Ida & Nakagoshi 1996, Ostfeld & Canham 1993, Pigott 1985,

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Sato 2000). Yet this 'stem-cutting', essentially a lethal form of browsing, remains unstudied in primary tropical forest except for some large mammals (e.g. pigs, Ickes *et al.* 2005).

Stem-cutting begets two pertinent and intriguing considerations. First, that co-occurring tree species are not equally vulnerable to it suggests that it could be non-random and selective. If so, interspecific differences in stem quality from physical and chemical traits in their wood or bark may deter, or attract, such attacks (Gill 1992). These traits might include stem density and fibre content (Alvarez-Clares & Kitajima 2009, Bozinovic *et al.* 1997), nutrients and minerals (Hansson 1991, Hjältén & Palo 1992), secondary plant metabolites (Bryant *et al.* 1991, Freeland & Janzen 1974, Lee *et al.* 1999), or even aromatic organic volatiles (Bedoya-Perez *et al.* 2014) cued upon by individuals especially active at night, namely rodents (Howard *et al.* 1968, Vander Wall 1998).

The second consideration is the habitat use of small mammals (Gill 1992), which can remove seeds faster in canopy 'gaps' created by treefalls than in the more closed-canopy areas of tropical rain forest (Norghauer & Newbery 2011, Norghauer *et al.* 2006, Schupp 1988). Indeed, liana tangles and dense vegetation of gaps may protect some rodent species from their predators to increase their fitness and abundance (Beck *et al.* 2004, Lambert *et al.* 2006, Malcolm 1995, Malcolm & Ray 2000), while the greater light there accelerates the recruitment of tree species across the shade-tolerance spectrum (Denslow 1987, Rüger *et al.* 2009) which is critical for understanding their regeneration dynamics and life-history strategies (Connell 1989, Hartshorn 1978).

This paper compares stem-cutting predation of two dominant, masting tree species that differ markedly in their population structures and shade-tolerance as seedlings. The incidence of stem-cutting in 40 gap-understorey areas and the species stem tissue traits were investigated to test three hypotheses: (1) Seedlings of each species are not equally prone to stem-cutting. (2) Such attacks are more common in gaps than nearby forest understorey. (3) The two species differ in key wood and bark traits, which might influence their vulnerability to stem-cutting by small mammals.

METHODS

Study site

The field research was done in lowland primary rain forest at Korup National Park, Cameroon, in and around the 82.5-ha permanent 'P-plot' (5°1'N, 8°5'E; 125 m asl) that is situated within a large grove of the canopy-emergent tree, *Microberlinia bisulcata* A. Chev. (Newbery *et al.* 1998, 2013). Here the soils are quite sandy and resource-poor, and especially deficient in P and K nutrients (Newbery *et al.* 1997). Annual rainfall is heavy, at *c.* 5100 mm, coming almost entirely during a 9-mo wet season (March–November; Newbery *et al.* 2006). Korup reportedly has 47 species of rodent; the giant pouched rat (*Cricetomys emini* Wroughton) is confirmed as present in the park and region (Norghauer pers. obs.; Fa *et al.* 2006).

Natural history

The population of *M. bisulcata* at the site is mixed with that of another dominant canopy-emergent species, *Tetraberlinia bifoliolata* (Harms) Haumann (Newbery *et al.* 2013). However, the adult trees of *T. bifoliolata* are smaller than those of *M. bisulcata* (≈125 cm vs. ≈220 cm maximum stem diameters), because they grow slower but also die faster than *M. bisulcata*, with seeds of both species ballistically dispersed during masting events (Norghauer & Newbery 2015). Early in development, however, the seedlings and saplings of *M. bisulcata* are much less tolerant of shade, yet can grow faster but also die faster than those of *T. bifoliolata* (Green & Newbery 2001, Norghauer & Newbery 2013, Norghauer *et al.* 2014). For both species, seed losses to small mammals are more likely in gap areas than in more closed-canopy areas of the forest (Norghauer & Newbery 2011). And without the extra light provided by gap areas, new seedlings of either species scarcely increase in height following establishment (Green & Newbery 2001, Norghauer & Newbery 2013). That animals occasionally cut down *M. bisulcata* seedlings is known (Green & Newbery 2002). Signs of such attacks are conspicuous (Figure 1): stems are cut near the ground floor, at ≈5–10 cm height, usually at an angle (Figure 1a, c) with teeth marks evident on thicker stems (Figure 1b–d). For unknown reasons part of the stem is often removed and occasionally found shredded a few metres away (Figure 1b) (Norghauer pers. obs.).

Field data on seedling predation

Incidence of stem-cutting was systematically recorded as part of a large insect herbivore exclusion experiment. This experiment applied fine-mesh cages and control tops to individual, new seedlings that had naturally established in 40 paired gap and understorey areas after the 2007 masting event (applied between 13 December 2007 to 13 January 2008; see Norghauer & Newbery 2013, 2014). The initial sample of *M. bisulcata* consisted of 97 seedlings per control and caged treatment; the sample size was smaller, at 46 seedlings per treatment, for the more dispersal-limited and less-fecund *T. bifoliolata* (Norghauer & Newbery 2015). All these seedlings were re-censused three times over *c.* 22 mo for their growth and mortality

Figure 1. Natural history photos of *Microberlinia bisulcata* seedlings established in gap areas that were damaged (encircled) by small mammals in rain forest at Korup, Cameroon. Shown are three stems cut (a); a stem that was cut and shredded thereafter (b); a stem cut but also partly chewed about the cutting point (c); a close-up of the characteristic angled cut made to a stem, with teeth impressions slightly visible, from small-mammal predators (d) (likely rodents (Muridae)).

(9–14 November 2008, 11–15 March 2009 and 4–10 October 2009: corresponding to the first full wet, second dry and second wet season, respectively). The key response variable here is whether or not a control seedling had its stem cut during this monitoring period (none was cut when caged). This subset of data also included 'replacements': same-aged, nearby wild seedlings added to the sample in the first or second re-census to replace control ones that had died (if possible) (see Norghauer & Newbery 2014).

Collection and preparation of stem tissues from a separate sample of seedlings

It is illegal to destructively harvest wild juvenile stems within Korup. However, in a parallel seed addition experiment, both study species had been dispersed artificially into gaps outside the main *M. bisulcata* grove, and these now large seedlings had to be eventually killed and removed. Hence, in the process, their bark and wood tissues were collected (full details in Appendix 1).

Stem tissue density. This trait is defined as the mass of a woody stem with its bark dried at 70°C for 72 h, divided by its 'fresh volume' (Pérez-Harguindeguy *et al.* 2013). Each 15-cm-long sample was measured twice, perpendicularly, for its diameter using digital callipers at five points: 2.5, 5.0, 7.5, 10.0 and 12.5 cm. At that point closest to a perfect circle, a 1-cm-wide disc centred on that measured point was removed. Its volume was calculated as $V = \pi r^2 h$; where r is the radius and h is the height. These volumes, though comparable between species, were not absolutely 'fresh'; some drying was needed to prevent fungal activity in the ≈4 wk between sample collection and arrival in Bern, Switzerland.

Tissue separation. From the now 14-cm-long samples, their bark was removed from stem wood using a kitchen knife cleaned with ethanol between sample separations. Bark and wood tissues – the latter cut into small pieces using clean shears – were fine-milled into a powder using a planetary micro-mill ('Pulverissette 7' by Fritsch GmBH, Germany). These samples (n = 56, from 14 locations) were dried once more for 18 h at 45°C and then stored in glass vials in a refrigerator (4°C) until used.

Nutrients. From each wood and bark sample, ≈300 mg (300–359 mg) and ≈20 mg (16.6–36.1 mg) respectively, were digested in a 2.5-ml mixture of selenium, sulphuric acid and salicyclic acid. These digestions were analysed for nitrogen (N) using the modified Bertholet reaction, and for phosphorus (P) with the molybdenum-blue one. Concentrations were determined colorimetrically on a Skalar San^{++} continuous flow auto-analyser (Skalar Analytical B.V., Breda, the Netherlands). The tissue concentrations of calcium (Ca), potassium (K) and magnesium (Mg) were determined using the same digests on an Optima 7000 inductively coupled plasma, optical emission spectrometer (ICP-OES; Perkin Elmer, Waltham, USA).

Total phenolics. Concentrations of total phenolic compounds were determined using an automated procedure. The tissue material is first mixed with a solution of carboxymethyl cellulose and EDTA (ethylenediamine tetra acetic acid); to this is added an alkaline ferric solution that in turn reacts with polyphenols to yield a red dye measured at 600 nm: this method has been found to be as robust as the more laborious Folin-Ciocalteu method (de Mattos & Zagal 2010). Phenolics were extracted from 16 mg of tissue samples in 60% methanol and stored at −20ºC. Phenolic concentrations were compared using gallic acid, GA, as the standard (3,4,5-trihydroxybenzoic acid, from Sigma-Aldrich, USA).

Non-volatiles. From each powdered sample, 10 mg was dissolved in 2 ml of a solution of 70% MeOH (HPLC grade), 29.5% H_2O (Milli-Q) and 0.5% formic acid ('puris'), in a 2-ml Eppendorf tube. Then, to each tube, 5−10 tiny glass beads were added and centrifuged for 4 min at 14 000 rpm; 1 ml of solution was removed and re-centrifuged as before; finally, 700 μl was pipetted into HPLC vials and stored at −20ºC until use. Extracts were analysed in an untargeted manner for low-molecular-weight primary and secondary metabolites. To separate and detect these compounds, ultra-high pressure liquid chromatography coupled to high-resolution mass spectrometry was used (UHPLC-HRMS; full details in Appendix 2).

Volatiles. Wood and bark powdered samples were stored in Eppendorfs, at −80°C, until analysed for volatile organic compounds using gas chromatography coupled to mass spectrometry (GC-MS). To do this, 1.5 mg of powder was accurately weighed and placed in microvial glass inserts (Gerstel GmBH), then placed into individual glass liners that were closed with metallic adaptors. To allow relative quantification of detected compounds, 1 μl of internal standard (solution of ethanol with 1% of cis-3-hexenyl acetate), was added manually in the upper part of each microvial, avoiding direct contact with the sample. All samples were further handled by a multipurpose GC-MS sampling system (MPS2, Gerstel GmBH, Mellinghofen, Germany) that positioned them randomly within the tray. The system was equipped with both a thermal desorption unit and a cooled injection system (TDU & CIS, Gerstel

GmBH) (full details in Appendix 2). Plastic scratched from inner Eppendorf was analysed as a corresponding control and determined which of the compounds were not of plant origin. In addition, blank analyses were conducted every five samples in order to clean the system.

Data analyses

Stem-cutting. The probability of an individual seedling having its stem cut was determined in a generalized linear mixed model (GLMM) that used the logit link and a binomial error distribution for the binary response (cut or not-cut). The GLMM considered the incidence of stem-cutting for the entire starting population of seedlings that died over the *c*. 2-y study period; it included canopy cover (gap vs. understorey) at the highest stratum, and then species (*M. bisulcata* vs. *T. bifoliolata*), and their interaction, as fixed terms. The model's random term was the 'block' of each pair of gap and understorey locations, and all variance components were estimated using restricted maximum likelihood (REML) with the default Schall-fitting algorithm in Genstat v. 16.2 (VSN International Ltd, UK). Model assumptions were checked using graphic diagnostics.

Tissue traits. To determine whether the species differed in stem tissue density, a paired *t*-test was used to control for any environmental influences on this trait. To test for nutrient and phenolic differences between species and between tissue types (bark vs. wood), or their interaction, an analysis of covariance (ANCOVA) was used. In these six ANCOVAs the covariate was seedling height, which in turn should reflect some of the major variation in light and soil resources among the gap locations. Indeed, re-analyses with linear mixed models gave near identical results (not shown): indeed, in all cases the 'block' variance component was less than its standard error so long as height was included in the models.

Non-volatiles and volatiles. To reduce, in an unbiased way, the many peaks detected in the data, a principal component analysis (PCA) was used. If a modest separation appeared in the PCA score plots, as found in all cases here, then a partial least squares discriminate analysis (PLS-DA) was performed. In this 'supervised', follow-up approach, the apparent separation is enhanced using a priori knowledge, or class predictors – in this case, species identity. However, because PLS-DA is prone to 'over-fitting', models were checked using cross-validation with R^2 and Q^2 metrics: the former should not greatly exceed the latter (Worley & Powers 2013) and values of $Q^2 > 0.4$–0.5 are considering reliably safe (Westerhuis *et al.* 2008). PCA and PLS-DA analyses were performed using Simca 13.0. After data processing, the most discriminating volatile organic compounds between species and tissues (i.e. wood vs. bark) were tentatively identified with the NIST11 mass spectral library (U.S. Department of Commerce), as well as the PBM search format (Agilent Technologies, Inc.).

In these wood analyses two samples – one *M. bisulcata*, and one *T. bifoliolata*, each from different locations – were accidentally cross-contaminated. These were removed and replaced with two spare samples, nearest to their location, to balance the analysis and presentation. One additional bark sample for *M. bisulcata* (the first processed) was manually cleaned of chemical contaminants not present in the other *M. bisulcata* samples.

It is worth highlighting here three aspects of our analysis which could inform future studies. Firstly, heating at 250°C for 6 min did not burn the stem tissue samples, and so should have revealed the most interesting and relevant species differences in volatile compounds in bark and wood. This is important because preliminary analyses at 320°C resulted in ashes after 6 min and a lot of irrelevant volatiles. Secondly, the insertion of an internal standard for quantification is strongly recommended because it is a robust way to evaluate the consistency of the GC-MS analyses (which were very accurate here). Thirdly, while the identified volatiles cannot be confirmed with 100% certainty, we are confident about their names since we used two databases, subtracted the noise of the chromatogram in each case, and considered only those matching between 80% and 99%.

RESULTS

Seedling predation

After 2 y, the percentage of the weakly shade-tolerant *M. bisulcata* seedlings that had died in the understorey (68%) was three times greater than that for the strongly shade-tolerant *T. bifoliolata* (23%) (Figure 2). In gaps, however, this species difference was more than four-fold, as very few seedlings of *T. bifoliolata* died there (47% vs. 11% respectively; Figure 2). However, only a single case of stem-cutting was recorded in the understorey, on *T. bifoliolata*, whereas in gaps it was responsible for 83% of *M. bisulcata* deaths, as it evidently killed 39% of all seedlings that had established there (Figure 2). In stark contrast, just two seedlings of *T. bifoliolata* were killed by stem-cutting in gaps (4.3%) of all that had established there. Accordingly, the likelihood of a stem being cut was significantly different between the two canopy types (GLMM, $F_{1,280.8} = 8.37$, $P = 0.004$) and between species ($F_{1,238.2} = 25.7$, $P < 0.001$). When examined on a monthly basis, the rate of stem-cutting in the first full wet season was 2.89% mo^{-1}; it was 2.03% mo^{-1} in the

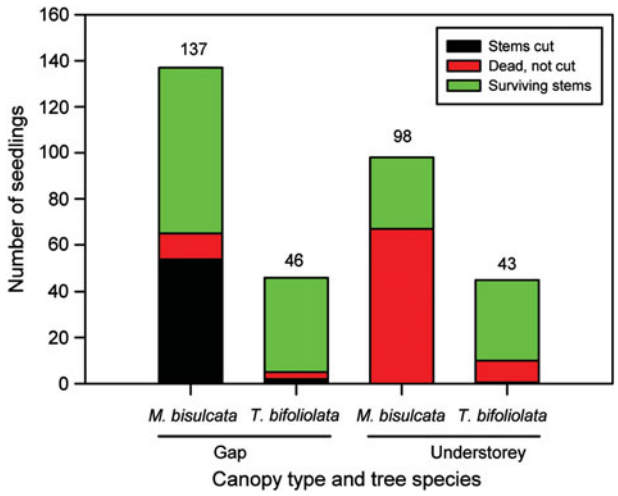

Figure 2. Stacked bars showing the absolute proportions of naturally established seedlings that died from stem-cutting vs. other causes in 40 paired canopy gap and understorey areas over the *c.* 2-y study period at Korup, Cameroon. The total sample sizes for the tree species *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* under each canopy type are given above each bar (these include any 'replacement' seedlings). Because of ballistic dispersal limitations, only 12 of the 40 gap-understorey areas had both species present for monitoring.

second dry season; and it was 3.17% mo^{-1} in the second wet season after the 2007 mast ended.

In addition, the random 'block' variance component had a value much greater than its SE (2.99 vs. 0.99): this revealed that some gap locations were more prone to stem-cutting than others in this forest (Figure 3). There was no circumstantial evidence that seedling stems of other tree species around cut *M. bisulcata* stems were also likewise predated. Might the degree of canopy disturbance, i.e. gap size, or proximity to one or more conspecific adult trees, explain this spatial pattern? A single, ad hoc analysis revealed that the proportion of cut stems did not increase significantly with percentage canopy openness measured in November 2008 when used as a proxy for gap size (generalized linear model, GLM, $F_{1,27} = 0.95$, $P = 0.34$), even after first accounting for gap's distance to the nearest adult — which itself was a negative, albeit not significant, predictor of cut stems ($F_{1,27} = 2.20$, $P = 0.15$). The final term in the model, adult basal area within a 50-m radius of gaps, was not significant either ($F_{1,27} = 0.03$, $P = 0.86$). Like the GLMMs for seedling survival, this GLM accounted for any over-dispersion in the data, but complete predictor data were available for only n = 33 (of the 34 gaps with *M. bisulcata*).

Tissue traits

Stem tissue density. The *M. bisulcata* seedlings had, on average, a 15% lower density than *T. bifoliolata* seedlings growing in the same gap locations (paired *t*-test, df = 13, $t = -5.17$, $P < 0.001$). Their mean values (± SE) (range) were, respectively, 0.551 ± 0.019 mg mm^{-3} (0.410–0.644 mg mm^{-3}) and 0.650 ± 0.024 mg mm^{-3} (0.414–0.749 mg mm^{-3}). These *M. bisulcata* seedlings had a mean height of 133 ± 22.8 cm and were slightly taller than their *T. bifoliolata* counterparts (120 ± 24.3 cm), but this difference was not significant (paired *t*-test, df = 13, $t = 1.88$, $P = 0.082$).

Nutrients and total phenolics. Bark concentrations of N and Na were similar between the two species, but twice that in wood (Figure 4a, f). For all other nutrients, whether or not the two species differed in their concentrations depended on the type of tissue (significant species × tissue interaction terms in ANCOVAs; Appendix 3). For instance, they differed in Ca and P only in their wood, but differed strongly in Mg and K in their bark (Figure 4b, c, e). In both tissue types, *M. bisulcata* contained more K than did *T. bifoliolata* seedlings, especially when bark was compared (Figure 4d). However, the seedling stems of *T. bifoliolata* contained more than two times the concentration of total phenolics than did *M. bisulcata* (Figure 4g). For *M. bisulcata*, all the nutrient and phenolic concentrations were much greater in its bark than wood. Though this tissue difference was not as pronounced for the nutrients in *T. bifoliolata*, it was more so for its phenolics. The seedling height of the samples was a significant covariate for explaining variation in N, P, K and Na but not Ca ($P = 0.250$), Mg ($P = 0.628$), or for total phenolics (0.919) (Appendix 3).

Non-volatiles. The PCA showed a clear separation between the two species, especially for bark (Appendix 4). The follow-up PLS-DA noticeably sharpened the species differences only for bark metabolites, especially along the first component axis (Figure 5a). Whereas the bark scores for *M. bisulcata* were more clustered than those of *T. bifoliolata*, this reversed for the wood scores (Figure 5b). Both PLS-DAs, however, were robust (bark, $R^2 = 0.99$, $Q^2 = 0.97$; wood, $R^2 = 0.96$, $Q^2 = 0.91$). However, upon closer inspection, only a few metabolites could be putatively identified as being typical of either species. For *T. bifoliolata*, these were: tetrahydroxyflavanone-rhamnopyranoside, tetrahydroxyflavan-pentahydroxyflavan (a dimer of flavonoid), dihydroyflavan-pentahydroxyflavan (another dimer), and pentahydroxyflavanone–rhamnopyranoside. For *M. bisulcata*, these were: hesperetin-7-O-sulphate (a sulphated flavonoid), and an unknown molecule ($C_{19}H_{26}O_{12}$). In sum, flavonoids were more abundant in *T. bifoliolata* than *M. bisulcata* seedling stems; this result matches that for total phenolics.

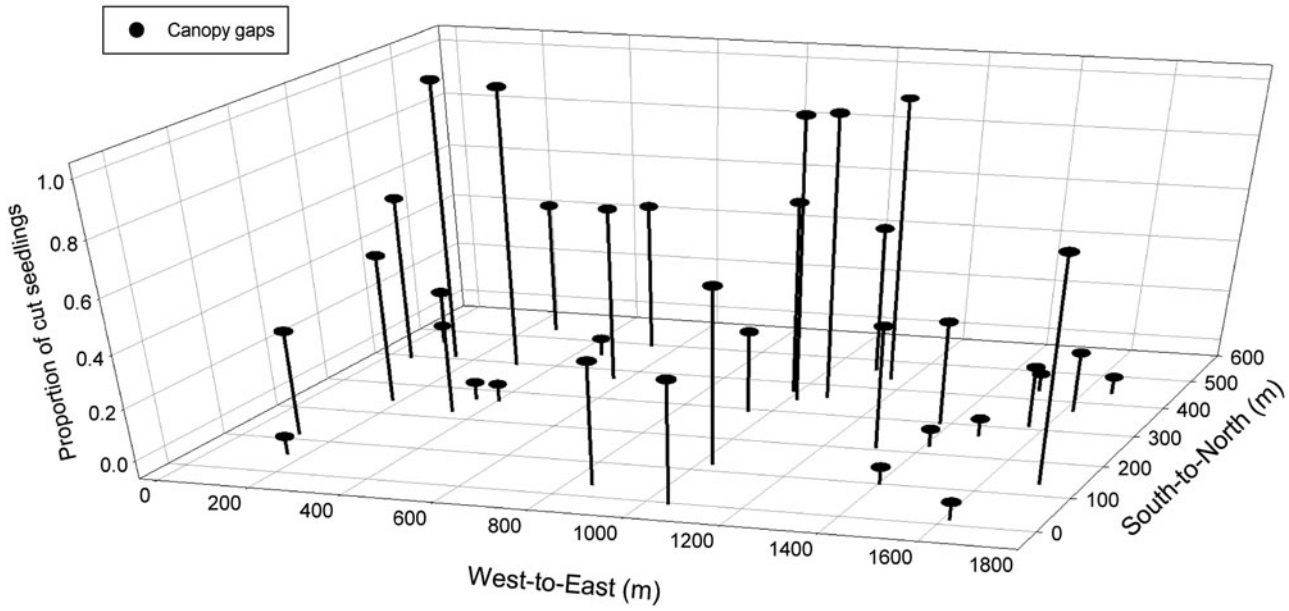

Figure 3. Spatial variation in the proportion of *Microberlinia bisulcata* seedlings (1–9 per gap area) that had their stems cut by small mammals during the c. 2-y monitoring period in the 82.5-ha P-plot at Korup, Cameroon. Each point represents a canopy gap location (n = 34 of 40 in total in the study; six gaps did not contain any naturally established *M. bisulcata* seedlings).

Volatiles. Species separation in the PCAs was evident, but weaker than that present for non-volatile metabolites (Appendix 4). For the bark samples the PLS-DA (Figure 5c) greatly improved the separation, and it was robust ($R^2 = 0.89$, $Q^2 = 0.69$). For the wood samples both species had less variation in their volatile profiles than they did for bark (Figure 5d) ($R^2 = 0.93$, $Q^2 = 0.87$). However, two *M. bisulcata* samples were outliers for unknown reasons, lying just outside the 95% confidence ellipse (Hotelling's: not shown).

Closer inspection identified the chromatographic peaks containing the most discriminant ions responsible for the species separations in the PLS-DAs. These key volatiles are listed in Appendix 5, along with their ecological activity in other taxa. Generally, many more fatty acids were present in *M. bisulcata* than in *T. bifoliolata* which in turn was clearly richer in phenolics.

DISCUSSION

Canopy disturbance increases seedling susceptibility to stem-cutting by small mammals

Stem-cutting predation was restricted almost entirely to *M. bisulcata* in gaps, but was virtually absent in the forest understorey for either tree species. There are two plausible explanations for this habitat effect. The first is that the small mammals responsible are simply resident in these gap areas and rarely venture beyond them to harvest seedlings in this way because of predation risks. For example, in Japanese beech forest, rodents gnawed many more beech and oak seedling stems growing amidst *Sasa* grass vegetation than without it (Ida & Nakagoshi 1996). Seeds of *M. bisulcata*, on the other hand, being nutritionally valuable and copious during masting events in this resource-poor forest (Newbery *et al.* 2006), are rapidly removed in the understorey (Green & Newbery 2002), albeit per-capita losses are still greater in gaps (Norghauer & Newbery 2011). The second explanation is that the small mammals responsible target gap areas because the resource quality of *M. bisulcata* is better there than in the understorey, where new seedlings cannot increase quickly in height and stem girth. Recall, that both tree species will remain stunted in the deep shade but they persist differently there (Green & Newbery 2001, Newbery *et al.* 2006, Norghauer & Newbery 2013). Preferential foraging in gap areas is not unheard of: several species of large browsing mammals do so in temperate forest (Kuijper *et al.* 2009). If plant size or quality determine risk of stem-cutting then it would be pertinent to know if surviving gap stems – now large relative to those suppressed in the understorey – are cut less often once gaps have closed up. To confirm the gap foraging/protective habitat preference suggested here, it would be necessary to survey small mammals in both habitats and to identify the agents of stem-cutting. This could be done via live- or camera-trapping small mammals, coupled to video footage of their behaviour (Jansen *et al.* 2004, Kuijper *et al.* 2009, Sato 2000), to help to reveal the reason(s) stems are cut.

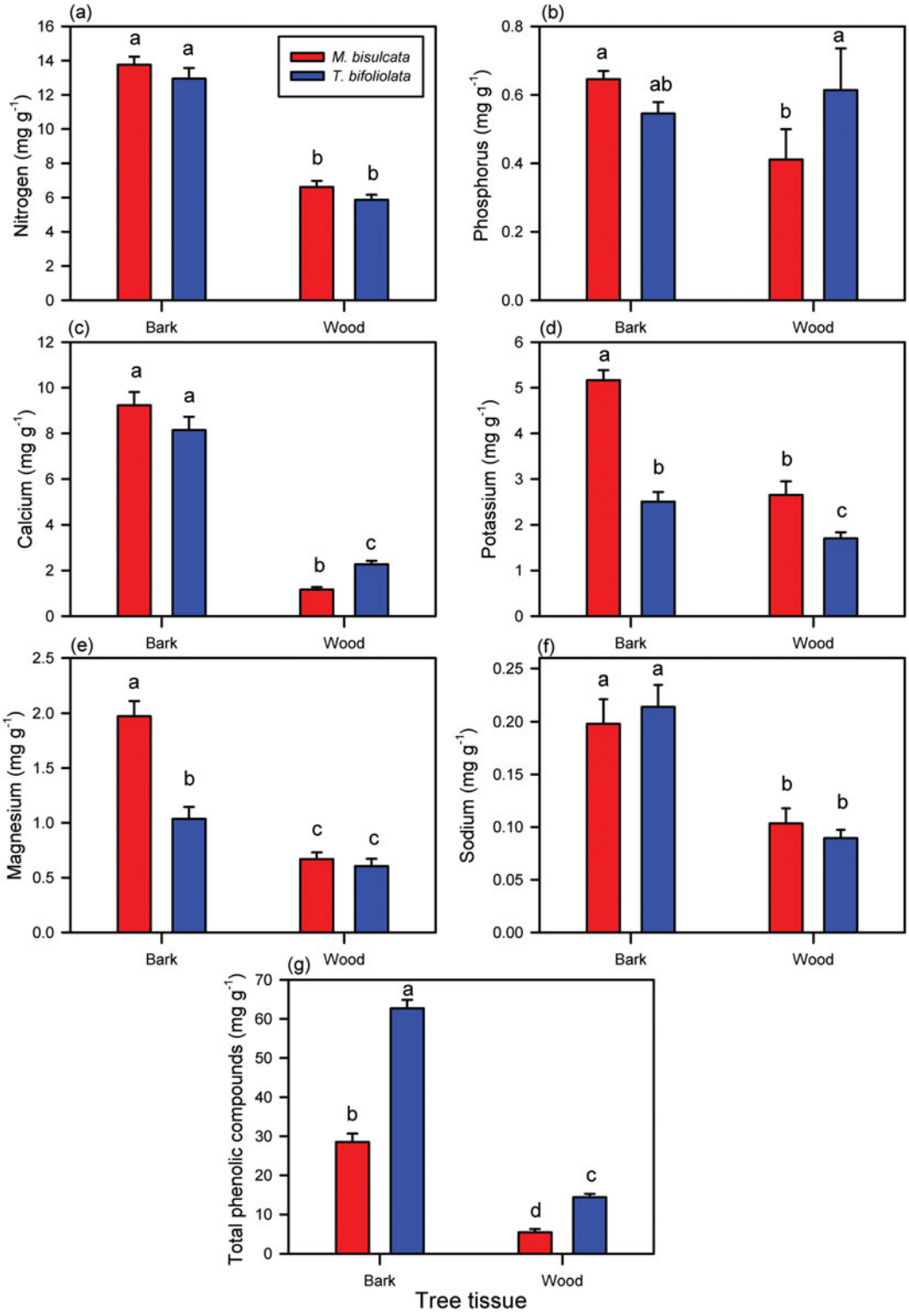

Figure 4. Concentrations of six nutrients (a–f) and that of total phenolic compounds (g) in the stem tissues of *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* tree seedlings growing in canopy gap areas at Korup, Cameroon. Phenolic compounds are expressed in gallic acid equivalents (GA). Bars are the unadjusted, raw means (± SE); those with different letters are significantly different using a LSD test at 5% following ANCOVAs (full statistics in Appendix 2).

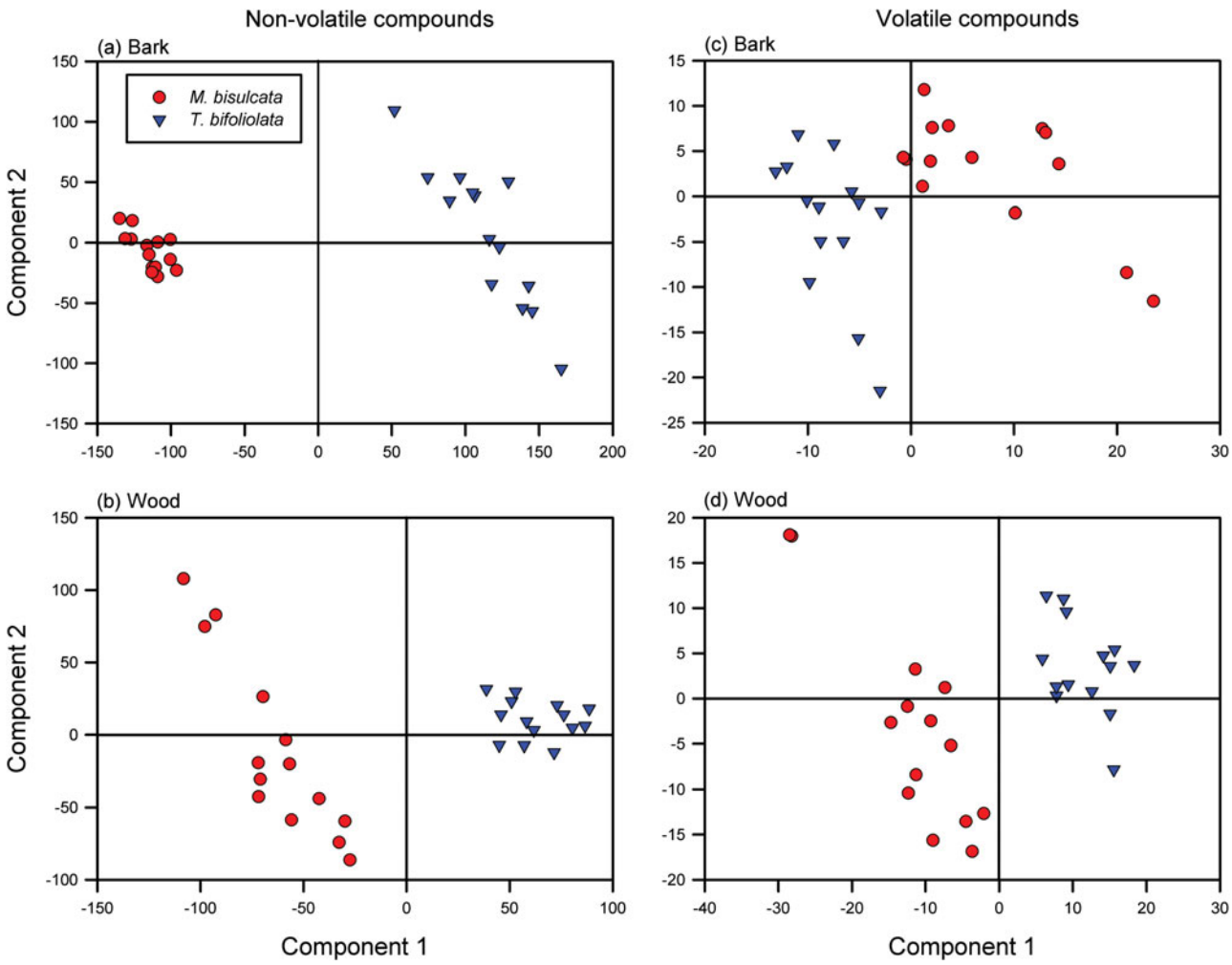

Figure 5. Scores of follow-up PLS-DAs (partial least squares discriminate analysis) performed on the secondary metabolite data. Comparisons of the species-specific chemical profiles of non-volatile (a, b) and volatile compounds (c, d) detected in the stem tissues of *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* tree seedlings grown together in canopy gaps at Korup, Cameroon. The percentage variance explained by components 1 and 2, respectively, were 37.3%, 5.0%; 22.0%, 11.3%; 25.7%, 17.4%; and 31.4%, 15.6%, respectively.

Indeed, it is unknown why small mammals would want to cut down growing seedlings in gaps. The most likely culprits are rodents, and in particular the widespread and large nocturnal giant pouched rat (*Cricetomys emini*) (Olayemi *et al.* 2012; body and tail length of *c.* 45 cm each weighing up to 1.4 kg, Kingdon 1997). We can only speculate on the reasons, which include: (1) to simply gnaw on stems to wear down their growing incisors and thus keep them short, as suggested by Watt (1919, 1923); (2) to ingest the bark/wood material to supplement their dietary needs (Bryant *et al.* 1991, Gill 1992, Pigott 1985, Weeks & Kirkpatrick 1978); (3) to use the stem portions cut and removed for nest-building in burrows (Watt 1919, 1923); and perhaps most interestingly, (4) to clean or disinfect their teeth or mouth, as suggested by the palmitic acid in *M. bisulcata* bark (Appendix 5 reference therein). This last might be the most plausible because if *M. bisulcata* stems are not actually ingested, rodents should prefer the tougher stems of *T. bifoliolata* to wear down their incisors. That they do not, coupled to the very wet environment at Korup favouring bacteria and fungi, instead suggests that *M. bisulcata* stems may provide a unique, yet easily found and chewable source of anti-microbial protection for their mouth (or nests).

The significant spatial variation in stem-cutting of *M. bisulcata* seedlings (Figure 3) could not be explained by either gap size or the neighbourhood of conspecific adult trees. Therefore, other unstudied factors may play a role in determining where sapling recruitment is 'safer' than others: this may include individual gap location relative to that of carnivores of small mammals, swamp areas, or other food resources used by small mammals. The results also suggest that following masting events, established seedlings are not killed in a distance- or density-responsive

way by small mammals (Janzen 1970); this is perhaps not surprising given the generalist diet of terrestrial vertebrate herbivores (Clark *et al.* 2012, Struhsaker 1997, Theimer *et al.* 2011). However, on a very coarse spatial scale, no stems were cut in gaps outside the adult *M. bisulcata* grove – this would make sense if the small mammals responsible were territorial, preferring to live within the *M. bisulcata* grove where seed-food inputs are frequent and large in masting events every 2–3 y.

Linking tree species traits to seedling stem-cutting

The stark contrast in stem-cutting between the tree species was mirrored by differences in some of their key physical and chemical traits. A 20% higher stem tissue density in the more shade-tolerant *T. bifoliolata* than in the light-demanding *M. bisulcata* is not surprising: this fits with prior work on both species' resistance traits (Norghauer *et al.* 2014), and with the general view of a growth-defence trade-off across species (Coley *et al.* 1985). It has been shown experimentally that, although *M. bisulcata* persists poorly in the shade, it could grow faster in height than *T. bifoliolata* in gaps were it not so susceptible there to leaf herbivory from insects (Green & Newbery 2001, Norghauer & Newbery 2013). Stem tissue density was very strongly correlated with early seedling survival at 7 mo for eight tree species studied in Panama (Alvarez-Clare & Kitajima 2007); it is also correlated with species' leaf density and lifespans as well (Kitajima *et al.* 2013). At Korup, the stem tissue density of seedlings and saplings may be especially important for surviving the wet season when thunderstorms cause much debris to fall from the canopy, and for resisting further breakage and trampling from large-bodied mammalian herbivores typical of African forest fauna. Clearly, stem lignification did not protect *M. bisulcata* seedlings from being cut, however (Figure 1), nor did it protect 1–2-y-old temperate beech (*Fagus crenata*) seedlings from rodents after masting events (Ida & Nakagoshi 1996). Nevertheless, there must be a threshold in stem girth after which the risk of stem-cutting in *M. bisulcata* becomes negligible because it is physically impossible, or inefficient energetically, for small mammals to do it. To confirm such an ontogenic shift in resistance will require long-term field study.

The strongest effects seen for species' nutrient differences were for K and Mg concentrations in their bark (Figure 4). Sodium (Na), known to be preferred by wood-gnawing temperate rodents (Hansson 1991, Weeks & Kirkpatrick 1978), cannot explain the preference of *M. bisulcata* over *T. bisulcata*, nor can calcium (Ca), phosphorus (P) or nitrogen (N). Likewise, Hjältén & Palo (1992) also concluded that N was not a deciding factor in the feeding preferences of voles and hares, which was better explained by species differences in the digestibility and phenolics of temperate tree branches and shoots. Thus, in this resource-poor forest, we cannot discount a nutritional role of K as well as one for Mg, which together might prompt small mammals to selectively forage for *M. bisulcata* seedlings at Korup. Unfortunately, there is generally little research into the relationship between bark minerals and consumption by rodents in native tree species, much less in tropical regions (Baxter & Hansson 2008).

The results also strongly point to much better resistance against herbivores in *T. bifoliolata* – and a lack thereof in *M. bisulcata*. That *T. bifoliolata* stems had higher total phenolic concentrations than those of *M. bisulcata* (Figure 4g), in addition to a very different composition of non-volatile secondary metabolites (Figure 5a,b), matches trends already found in their leaf tissues (Green & Newbery 2001, Norghauer *et al.* 2014). Many of the volatile compounds detected in *T. bifoliolata* are linked to anti-herbivore or anti-pathogenic effects in other taxa, mainly insects (Appendix 5), and there is a vast accumulated literature on the role of secondary metabolites in woody plant defence against mammalian herbivores (Bryant *et al.* 1991, Freeland & Janzen 1974). For instance, experimental work has shown that two rodent species in Chile prefer food items low in both fibre *and* tannins (Bozinovic *et al.* 1997). Moreover, eugenol and cinnamaldehyde exhibited moderate and potent activity respectively as repellents against gnawing by mice (Lee *et al.* 1999), and both of these, or their variants (excluding methoxyeugonol), were present in the bark and wood, respectively, of *T. bifoliolata* seedlings only (table in Appendix 5; 'sinapaldehyde' is the name given to 3,5 dimethoxy-4-hydroxycinnamaldehyde).

The tree species' volatile profiles are particularly intriguing in this context (Appendix 5). If small mammals combine taste and odour to learn to avoid toxic woody plants (Bryant *et al.* 1991), then, when foraging for *T. bifoliolata* stems, their initial encounter with bark seems to be of utmost importance. It is noteworthy that while *T. bifoliolata* bark is characterized by terpenes and phenols, likely making them unpalatable to herbivores, *M. bisulcata* lacked any of these putative protective compounds; conversely, the fatty substances in its bark may attract rodents because of their nutritive value (Hansson 1973). Finally, if *M. bisulcata* is preyed upon at night, as suggested here, sight becomes less important than smell and taste cues for small mammals. When the bark of *M. bisulcata* gap seedlings is scratched, a conspicuous scent is elicited that smells like topical menthol/methyl salicylate ointment (Norghauer, pers. obs.) – we hypothesize that the volatile 3-methypentanal found in the bark of *M. bisulcata* may act as an olfactory cue for their location by small mammals. A plant volatile need not only be elicited at high temperature (Bryant *et al.* 1991), or following herbivore attack, but may also serve as a reliable foraging cue for

mammalian herbivores if it is ubiquitous even at very low concentrations (Bedoya-Perez *et al.* 2014).

Whether it is one trait primarily, which is doubtful, or rather a synergistic combination of stem tissue density and their chemical content that determined the avoidance of *T. bisulcata*, and preference for *M. bisulcata*, by small mammals cannot be known without experiments and *in situ* bioassays that explore the main and interactive effects of these putative defensive compounds.

Implications for *Microberlinia bisulcata* populations

We have no data on the abundance of rodents inside or outside the *M. bisulcata* grove, or how it might fluctuate over years. It is unlikely that their populations are stable, however (Struhsaker 1997) – they may spike soon after masting by *M. bisulcata* (which happens every 2–3 y, Newbery *et al.* 2006). By removing *M. bisulcata* from gaps, which are those very habitats essential for its growth into larger-size classes, these predators function to diminish the abundance and frequency of its seedlings able to become saplings, and therefore should curb recruitment rates. Over time, this should limit the sapling bank further than it already is by the canopy disturbance regime. As such, we suggest that this rodent behaviour can make an important contribution to species coexistence beyond the seedling stage by pre-empting competition between the dominant, fast-growing *M. bisulcata* and other tree species for winning space and other resources in gaps. A prominent role for small mammals limiting the recruitment of seedlings from seed was recently found in another African forest, in the Congo Basin (Clark *et al.* 2012, also see Struhsaker 1997). In the case of *M. bisulcata* it would appear that stem-cutting impinges upon the fitness benefits associated with a masting reproduction strategy, if the aim is to satiate its predators after dispersal and not before. An expected increased in rodent abundance after masting may increase predator pressure on those established seedlings that escaped seed predation via successful satiation in gaps (Norghauer & Newbery 2011).

We anticipate that regeneration of remnant *M. bisulcata* in forest logged of other target species is at further risk from stem-cutting because logging generally has a positive influence on rodent abundance and richness (Lambert *et al.* 2006, Malcolm 1995, Malcolm & Ray 2000, Struhsaker 1997). That said, in heavily logged forest the giant pouched rat might not be common because of unsuitable habitat (Struhsaker 1997) or high hunting pressure (Fa *et al.* 2006). Finally, efforts at restoring this critically endangered tree species (IUCN category A1c + 2c) in secondary or otherwise disturbed forests should consider protecting newly planted seedlings with cages, and surrounding any small populations of *M. bisulcata* trees with logging-free buffer areas.

Stem-cutting, as reported here, is not well documented from tropical forests. In several field studies of vertebrate exclusion in the Neotropics and Australia, the impact on seedling survivorship was either short-lived, within the first 2 mo, or the main cause of death was uprooting of the seedling for seeds and/or cotyledons to eat (Osunkoya *et al.* 1993, Paine & Beck 2007, Sork 1987, Theimer *et al.* 2011). Some stem-cutting was noted in seedlings of six Panamanian species, but these were studied only in the understorey (Alvarez-Clare & Kitajima 2009). Without more investigation, it is too early to know if the high prevalence of stem-cutting on *M. bisulcata* may not only reflect stem traits associated with its life-history but perhaps also a geographic association with small mammals, namely rodents, endemic to African rain forest.

CONCLUSIONS

Our results point to tree species trait differences and habitat use by small mammals, likely rodents, as determining the selective stem-cutting of *M. bisulcata* seedlings in forest gaps. As such, in addition to other biotic and abiotic factors, stem-cutting predation is another contributing factor that helps explain the dearth of *M. bisulcata* saplings at Korup. Hopefully these results will entice tropical ecologists, foresters and zoologists to view small mammals a little differently, the rodents particularly, and spur field investigations of their functional role as predators in the seedling-to-sapling stages of other co-occurring tree species. It would be highly germane to know if rodents attack other dominant canopy tree species that share wood and bark traits with the fast-growing, weakly shade-tolerant seedlings of *M. bisulcata* – and likewise avoid very shade-tolerant, highly resistant tree species like *T. bifoliolata*.

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Appendix 1. Details on the collection of stems used in the trait analyses from a separate sample of seedlings of the two study tree species in gaps at Korup, Cameroon.

A seed addition experiment had used both study species to investigate their seed losses to small mammals inside and outside the main *M. bisulcata* grove (see Norghauer & Newbery 2011 for full details). Outside the grove there were no signs of stem-cutting at the 15 (formerly) 'gap' locations, from where the surviving stems in the paired control and fenced-exclusion quadrats 2.5 m apart (edge to edge) were measured for their heights (21–26 January 2014). From either of the two quadrats, two seedlings – one of each species – that matched closest in height were selected; a 15-cm-long portion of their stem (beginning at ≈5 cm height above ground) was removed, affixed with a tag, and stored in a perforated plastic bag in a waterproof box. This was possible at 13 of 15 gap locations where both species were still present (a spare set was taken at one location); at a 14th location, samples were instead obtained from the paired 'understorey' location where a tree had fallen to create a new gap. (A second set of spare samples was obtained here.) The samples were oven-dried at 40°C for 36–48 h (22–28 January 2014), then packaged with silica gel and flown to Bern, Switzerland, where they were oven-dried at 45°C for 24 h (17 February 2014), and stored with silica in a freezer at −20°C until later analyses. Because these tissue samples, unavoidably, came from gap stems older (≈6.5 y) than those on which clipping was actually recorded (≈2.5 y at most) we assumed that species trait differences did not vary substantial through their development up *c.* 130 cm height (on average) when still vulnerable to small-mammal stem-cutting.

Lacking electricity on the collection site, it was impossible to collect the samples using portable freezers in the rain forest of Korup. Therefore some very volatile organic compounds were likely lost during sample collection and preparation (i.e. modest drying). Nonetheless, in the absence of very high heat (>100ºC) it was anticipated that each species retained its characteristic volatile fraction in the samples.

Appendix 2. Further details on the methods used to detect non-volatile and volatile compounds in the stems of *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* seedlings at Korup, Cameroon.

Non-volatiles

Chemicals, water, acetonitrile and formic acid used for metabolite profiling were of UPLC-MS grade (Biosolve, Valkenswaard, the Netherlands).

Metabolite profiling

Untargeted metabolite profiling was performed on an Acquity UPLC™ from Waters (Milford, MA, USA) coupled to a Synapt G2 quadrupole time-of-flight mass spectrometer (Waters). The analytical conditions were as follows. Ultra-high-pressure liquid chromatography: column, Acquity BEH C18 50 × 2.1 mm i.d., 1.7-μm particle size (Waters); solvent system, A: water (0.05% formic acid), B: acetonitrile (0.05% formic acid); gradient program, 2%−35% B in 3 min, 35−100% B in 3 min, 100% B for 1.5 min, re-equilibration at 2% B for 1.5 min; flow rate, 600 μl min^{-1}; column temperature, 40°C; injection volume, 2.5 μl. Mass spectrometer: positive ion electrospray nebulization, capillary voltage 2800 V, cone voltage 25 V, source temperature 120°C, desolvation gas flow 800 l h^{-1}, desolvation gas temperature 400°C, acquisition in MSE mode over the range 85–1200 Da. The software used for data analysis was Masslynx 4.1 (Waters).

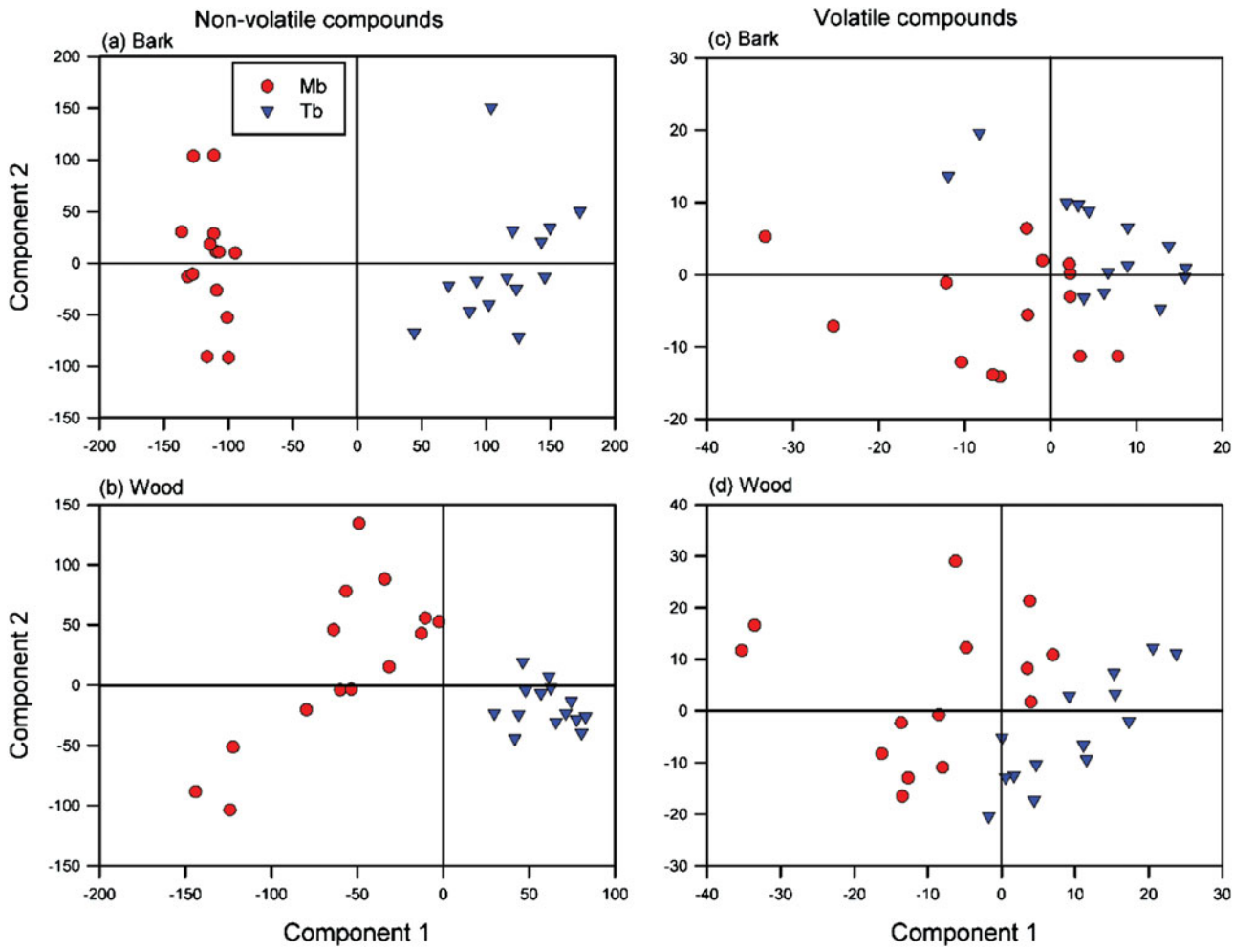
Metabolomic data were treated using Markerlynx XS™ (Waters) using the following parameters: initial and final retention times 0.0–7.6 min, mass range 100–1200 Da, mass tolerance 0.02 Da, retention time tolerance 0.06 min, intensity threshold 400 counts, automatic measure of peak width and peak-to-peak baseline noise, de-isotoping function applied. The obtained peak list was Pareto-scaled prior to multivariate analysis.

Volatiles

In the TDU (split-less mode), the samples were kept at 50°C for 0.2 min before an increase to 250°C at a rate of 640°C min^{-1} (hold time 6 min). The emitted volatiles were cryo-focused with liquid nitrogen (−80°C) in the CIS before being heated at 12°C s^{-1} to 270°C (hold time 6.5 min) and injected onto the GC column. The PTV inlet was operated in the solvent vent mode, with a vent pressure of 14 psi, a vent flow of 50 ml min^{-1}, and a purge flow of 50 ml min^{-1}. Compounds were separated on Agilent HP-1MS columns (30 m length × 0.25 mm i.d. and 0.25-μm film thickness). The helium carrier gas flow rate was 1.3 ml min^{-1} (constant flow mode). The temperature program of the GC operation was 50°C for 0.01 min, then increased to 260°C at a rate of 7°C min^{-1} (hold time 5 min), followed by a 2 min post run at 270°C. In all cases, the MSD transfer line temperature was set at 280°C and the ion source and quadrupole temperatures were set at 230°C and 150°C, respectively. Electron impact (EI) mode was used with a scanning over the mass range of 33–350 amu.

Appendix 3. The ANCOVA statistics for concentrations of nutrients and phenolics in the seedling stems of *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* trees in gaps at Korup, Cameroon. One *T. bifoliolata* sample of bark tissue digest was insufficient for the phosphorus analyses; concentrations were log-transformed for calcium and phosphorus analyses (the latter, first multiplied by 100) and for which two bark samples of *T. bifoliolata* were unusable (one was accidently contaminated and the other too low in mass). Height is of each seedling sampled.

Response	Sources of variation	df	m.s.	F value	P value
Nitrogen	Species	1	10.6	4.77	0.034
	Tissue	1	711	320	<0.001
	Species × Tissue	1	0.0001	0.000	0.980
	Height (covariate)	1	29.5	13.3	<0.001
	Residual	50	2.22		
	Total	54			
Phosphorus	Species	1	0.0201	0.510	0.480
	Tissue	1	0.386	9.74	0.003
	Species × Tissue	1	0.226	5.61	0.022
	Height (covariate)	1	0.445	11.2	0.002
	Residual	50	0.0396		
	Total	54			
Calcium	Species	1	0.0306	2.14	0.149
	Tissue	1	6.17	432	<0.001
	Species × Tissue	1	0.162	11.4	0.001
	Height (covariate)	1	0.0193	1.35	0.250
	Residual	51	0.0143		
	Total	55			
Potassium	Species	1	47.4	74.9	<0.001
	Tissue	1	38.4	60.7	<0.001
	Species × Tissue	1	10.2	16.0	<0.001
	Height (covariate)	1	3.60	5.68	0.021
	Residual	51	0.633		
	Total	55			
Magnesium	Species	1	3.55	25.4	<0.001
	Tissue	1	10.5	75.4	<0.001
	Species × Tissue	1	2.66	19.1	<0.001
	Height (covariate)	1	0.0331	0.240	0.628
	Residual	51	0.140		
	Total	55			
Sodium	Species	1	0.000006	0.000	0.969
	Tissue	1	0.170	44.7	<0.001
	Species × Tissue	1	0.00358	0.94	0.338
	Height (covariate)	1	0.0193	5.07	0.029
	Residual	49	0.00381		
	Total	53			
Total phenolics	Species	1	647	171	<0.001
	Tissue	1	178	472	<0.001
	Species × Tissue	1	220	58.7	<0.001
	Height (covariate)	1	0.400	0.0100	0.919
	Residual	51	37.8		
	Total	55			



Appendix 4. PCAs for non-volatile and volatile organic compounds in seedling stems of *Microberlinia bisulcata* and *Tetraberlinia bifoliolata* trees in gaps at Korup, Cameroon.

Appendix 5. Tabulation of the key volatile organic compounds isolated from seedling bark and wood tissues of two rain-forest tree species, *Microberlinia bisulcata* and *Tetraberlinia bifoliolata*, at Korup, Cameroon. Grouped volatiles are sorted by ascending retention times (r/t). HIPV refers to a herbivore induced plant volatile. The cited numbered references follow the table.

Tissue Species	Molecule	r/t (mean)	Compound class	Formula	Ecological function
Bark					
M. bisulcata	3-Methylpentanal	2.19	Aldehyde	$C_6H_{12}O$	Unknown. The closely related 2-Methylpentanal is a natural stimulant in the rodent main olfactory bulb[76]
	Furfural	2.61	Aldehyde	$C_5H_4O_2$	Fungicide[1,12], insecticide[1], nematicide[12], aromatic/fragrant (papaya)[11], released upon mechanical wounding[13]
	Myristic acid	18.20	Fatty acid	$C_{14}H_{28}O_2$	Nematicide[1], insecticide[2] HIPV** enemy attractant[15], antimicrobial oral activity (human)[4,5], antibacterial/antifungal[66,67,68]
	Palmitic acid	21.05	Fatty acid	$C_{16}H_{32}O_2$	Nematicide[1], parasitoid infochemical[3], antimicrobial oral activity (human)[4,5], mammalian micronutrient[7], pollinator attractant (Hymenoptera)[52], antibacterial/antifungal[66,67,68]
	Olealdehyde	25.24	Fatty aldehyde	$C_{18}H_{34}O$	Pollinator attractant[50], behavioural pheromone (stingless bees)[51], fatty flavouring agent (humans)[53], leaf-oil mite deterrent[54]
T. bifoliolata	Coumaran	8.73	Terpene	C_8H_8O	Neural toxicity to insects[8,] anti-feedant[9], plant defence against insects[10,48], insect repellency[74]
	Resorcinol	10.16	Phenolic	$C_6H_6O_2$	Antibacterial[1,21], fungicide[1,10], alleochemical[21]
	Eugenol	11.18	Phenolic	$C_{10}H_{12}O_2$	Insecticide[1, 16,17,19,20,38], fungicide[1,19,38,40], antibacterial[1,19,40], antiviral[19], antifeedant[1], anti-termite[19], nematicide[1,38], aromatic/fragrant (banana)[14], pollinator attractant[18], bee attractant[34], general resistance[10], antignawing activity[78]
	trans-Isoeugenol	12.80	Phenolic	$C_{10}H_{12}O_2$	Insecticide[16,17,19,20,38], pollinator attractant[18], bee attractant[34]
	Lupeol	29.58	Terpene	$C_{30}H_{50}O$	Antiviral[1], antimalarial[1], antiprotozoa[21], antimicrobial[21,62] antifeedant[22,25], insect deterrent[23], protective wax[24], plant defence against insects[48], insecticide[62]
	Lignoceric alcohol	31.98	Fatty alcohol	$C_{24}H_{50}O$	Lacks anti-microbial activity[26], insect behavioural cue[27,28]
Wood					
M. bisulcata	Cyclopropanemethanol	5.95	Alcohol	C_4H_8O	Antifungal[30], insecticide[30] sweet odour[31], anti-pathogenic[29]
	2-Methoxy-4-vinylphenol	10.48	Phenolic	$C_9H_{10}O_2$	Aromatic/fragrant (nutty-like)[32,33], found in a leaf extract[66], antioxidant[1]
	Methoxyeugenol	16.81	Phenolic	$C_{11}H_{14}O_3$	Bee attractant[34], antimicrobial[35,39] antibacterial[38], aromatic/fragrant(banana)[37], antifeedant[38], insecticide[38], antifungal[38]
	Coniferol	17.34	Phenolic	$C_{10}H_{12}O_3$	Avian repellent[36], lignin cell-wall component[58,59]
	Palmitic acid	21.07	Fatty acid	$C_{16}H_{32}O_2$	Nematicide[1], parasitoid infochemical[3,] antimicrobial oral activity (human)[4,5,] mammalian micronutrient[7], pollinator attractant (Hymenoptera)[52], antibacterial/antifungal[66, 67, 68]
	Oleic acid	23.34	Fatty acid	$C_{18}H_{34}O_2$	Mammalian micronutrient[7], parasitoid infochemical[3], antibacterial/antifungal[66, 67, 68]

Appendix 5. continued.

Tissue Species	Molecule	r/t (mean)	Compound class	Formula	Ecological function
T. bifoliolata	1-Penten-3-one	2.25	Ketone	C_5H_8O	Aromatic/pungent/bitter taste (green olives)[41,42], HIPV[43,44]
	Furfural	2.66	Aldehyde	$C_5H_4O_2$	Fungicide[1,12], insecticide[1], nematicide[12], aromatic/fragrant (papaya)[11], released upon mechanical wounding[13]
	5-Methylfurfural	4.14	Aldehyde	$C_6H_6O_2$	Attracts pyrophilic beetles[45], non-repellent (honeybees)[46], aromatic/fragrant (almond-like)[47]
	2,4-Dihydroxy-2,5-dimethyl-3(2H)-furan-3-one	4.58	Ketone	$C_6H_8O_4$	In honey[63], flower[64], and leaf extracts[65]; antioxidant[1], aromatic/food flavouring ingredient (strawberry)[75]
	Cyclopropanemethanol	6.04	Alcohol	C_4H_8O	Antifungal[30], insecticide[30], sweet odour[31], anti-pathogenic[29]
	Catechol	8.79	Phenolic	$C_6H_6O_2$	Antiviral[1], alleochemical[1], animal toxicity[49], plant defence against insects[10,14, 48]
	trans-Isoeugenol	12.80	Phenolic	$C_{10}H_{12}O_2$	Insecticide[16,17,19,20], pollinator attractant[18], bee attractant[34]
	Syringaldehyde	15.96	Phenolic	$C_9H_{10}O_4$	Antioxidant[1,71], insect communication[69], antimicrobial[70,71], antibacterial[56,71]
	Methoxyeugenol	16.88	Phenolic	$C_{11}H_{14}O_3$	Bee attractant[34], antimicrobial[35], antibacterial[39], aromatic/fragrant(banana)[37], antifeedant[39], insecticide[39], antifungal[39]
	Coniferaldehyde	17.09	Phenolic	$C_{10}H_{10}O_3$	Antibacterial[56], antifungal[57], incorporated into lignin[72], tree cell-wall component[58,59]
	Desaspidinol	17.68	Phenolic	$C_{11}H_{14}O_4$	Antimicrobial[55], antibacterial[77]
	Myristic acid	18.16	Fatty acid	$C_{14}H_{28}O_2$	Nematicide[1], insecticide[2] HIPV enemy attractant[15] antimicrobial oral activity (human)[4,5], antibacterial/antifungal[66,67,68]
	Pentadecanoic acid	19.61	Fatty acid	$C_{15}H_{30}O_2$	Wood-inhabiting fungi[60,61], antibacterial/antifungal[66,67,68]
	Sinapaldehyde	20.64	Phenolic	$C_{11}H_{12}O_4$	Antibacterial[56], antifungal[73], incorporated into lignin[72]

Appendix 5 continued. List of references for the cited ecological functions in the table above.

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