Modular, hollow culms of rain-forest bamboos explain their persistence across a wide range of light environments

Junichi Fujinuma[1,2,3,*], Matthew D. Potts[4], Abd Rahman Kassim[5], Rhett D. Harrison[6], Abd Razak O.[5] and Takashi S. Kohyama[3]

[1] Tropical Biosphere Research Center, University of the Ryukyus, Nishihara, Okinawa, Japan 903-0213

[2] Department of Forest Sciences, P.O. Box 27, FI-00014, University of Helsinki, Finland

[3] Graduate School of Environmental Science, Hokkaido University, Sapporo, Japan 060-0810

[4] Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720, USA

[5] Forest Research Institute of Malaysia, 52109, Kuala Lumpur, Malaysia

[6] World Agroforestry Centre, East and Southern Africa Region, 13 Elm Road, Woodlands, Lusaka, Zambia

Abstract: Tropical bamboos persist in a wide range of light conditions and quickly respond to changes in light availability. However, the mechanisms underpinning this ability remain unknown. In order to test the hypothesis that the modular and hollow culm architecture of bamboos explains their performance in a wide range of light environments, we determined the allometric relationships of two dominant bamboo species of the upper hill dipterocarp forests of Malaysia, *Gigantochloa ligulata* (n = 29) and *Schizostachyum grande* (n = 25), via destructive sampling. We also monitored biomass turnover of bamboos and woody trees in 24 permanent plots (1.92 ha in total) over a one-year period. Compared with woody trees, bamboo culms attained 1.5 times the height and their clumps supported four times as much total leaf area at the same above-ground biomass. In addition, at a given height, bamboo clumps had six times larger crown projection area than trees while having a similar amount of total leaf area per unit of crown projection area. Finally, bamboos' biomass turnover rate was three times higher than trees, and *G. ligulata* increased its specific rate of biomass increase after canopy disturbance, while trees decreased. We conclude that the unique architecture of bamboos allows them to persist under closed forest canopy light conditions and to respond to gap formation via high biomass turnover rate.

Key Words: allocation, allometry, clonal plant, clumping bamboo, coexistence, demography, morphology, sympodial branching, tropical forest

INTRODUCTION

In primary and secondary rain forests in South-East Asia and South America, bamboo species often account for a substantial fraction of the plant diversity (Bystriakova *et al.* 2003, 2004). In tropical lowlands, bamboos are usually restricted to disturbed sites (Gagnon 2009, Smith & Nelson 2011, Zhang & Cao 1995) or riparian habitats, and are rarely found in lowland primary rain forests. In contrast, in hill and montane forests, indigenous bamboo species are common components (Bystriakova *et al.* 2003, 2004; Dransfield 1992, Wong 1995). Bamboos that coexist with woody trees in these forests occur over a wide range of light conditions, from dark understorey to fully lit clear-cut sites.

Since bamboos seldom reach the tall top canopy layer of tropical rain forests (Widmer 1998, Wong 1995), their persistence depends on the ability to survive in the low-light understorey or to colonize high-light canopy gaps. However, unlike gap-dependent tree species, bamboos often lack effective seed dispersal mechanisms as well as dormancy (Bellairs *et al.* 2008, Janzen 1976, Wong 1995), which would limit their ability to exploit gaps by sexual reproduction. Many bamboo species thus dominate tropical rain forests after disturbances by means of vegetative propagation. They increase clump (genet) size by recruiting culms (ramets) via rhizome branching. The clumped genet structure of tropical bamboos, however, limits their ability to exploit gaps by horizontal vegetative growth. There remains an open question about what exact mechanisms enable bamboos to establish in canopy gaps and to survive under a closed

* Corresponding author. Email: juni.fujinuma@gmail.com

canopy (Swaine & Whitmore 1988). Previous studies hypothesized that the capability of bamboos to exploit a wide range of light conditions is explained by plasticity in leaf traits (Montti *et al.* 2014, Yang *et al.* 2014) and in genet architecture (Widmer 1998) since photosynthetic capacity of bamboos does not differ substantially from co-occurring woody trees (Bai *et al.* 2011, Dierick *et al.* 2010, Saha *et al.* 2009).

An alternative hypothesis is that bamboos' hollow culm and modular growth contribute to efficient light capture across a wide range of light conditions. Bamboo culms are hollow with internal cross walls that require less biomass to attain a given height and are robust against bending as compared with solid stems. Such hollow stem architecture is impossible for woody trees as they extend stem-wood area by peripheral cambial growth. In addition, construction of bamboo culms relies mostly on subsidized carbohydrates from other ramets within a genet for rapid elongation of culms (Kleinhenz & Midmore 2001). Bamboos, thus, maintain their crowns dynamically by replacing short-lived ramets that do not grow after initial shoot expansion (Franklin *et al.* 2010).

In this study, we tested the specific hypothesis that the hollow culms and modular architecture of bamboos are more efficient in light capture than woody trees so that photosynthetic gain of an individual ramet compensates for the construction costs of short-lived ramets allowing for the quick regulation of their clump structures as light availability changes. We tested this hypothesis by quantifying the architecture and biomass dynamics of two dominant clumping bamboo species, *Gigantochloa ligulata* and *Schizostachyum grande*, in comparison with those of co-occurring trees, in a hill dipterocarp forest in Peninsular Malaysia. Given that the light intensity declines from canopy surface to understorey, the crown foliage height determines available light resources. We evaluated the efficiency of light capture by quantifying above-ground architecture of bamboos and woody trees as a function of total above-ground biomass and crown height. Finally, we estimated biomass using allometric equations, and estimated demographic biomass turnover rates based on repeated censuses of permanent plots set along a disturbance gradient created by experimental timber harvesting.

METHODS

Study site

We carried out field research at Temenggor Forest Reserve in Perak State, Malaysia. The forest reserve is located in the northern part of Titiwangsa Mountain Range in Peninsular Malaysia. The study site covered 200 ha of the reserve (600–800 m asl with average slope of 27.5°),

with the main ridge running from east to west dividing the southern and northern slopes (Appendix 1). Annual rainfall at the study site recorded by the Forest Research Institute Malaysia (FRIM) in 2011 was 2215 mm, which was in line with the long-term range of 2000–3000 mm y^{-1} observed in the town of Gerik, 80 km west from the study site (Azmi & Sukumaran 2002). Rainfall exhibited moderate seasonality; November to March experienced more rain than the other months (Azmi & Sukumaran 2002). Primary upper hill dipterocarp rain forest, which typically has 50-m-tall emergent trees and 30–35-m-tall continuous canopy surface, characterized the forest reserve.

Permanent study plots were established in 2008 as a part of an experimental logging project led by FRIM. The reduced-impact logging was conducted by Perak Integrated Timber Complex, a state-owned logging company (Yap 2010), which created a wide gradient of canopy conditions from intact to almost clear cut. Prior to timber harvesting, FRIM established 24 rectangular plots each 20 m wide by 80 m long (3.84 ha in total) distributed on both sides of slopes in the study site (Appendix 1). A census of all the individual trees with $D_{tree} \geq 5$ cm (Table 1) in 2008 recorded 3212 stems representing 422 woody tree species (65 families) in 3.84 ha and a basal area of 36 m^2 ha^{-1}. Timber harvesting was carried out in 2010. As a result of a planned timber harvesting experiment, most of the 24 plots experienced partial loss of canopy cover. Approximately 12 mo after the tree harvesting, in 2011 and 2012, we conducted field observations of bamboos.

Studied bamboo species

Four bamboo species occurred within the permanent plots. We chose the two most abundant species in terms of ramet density (with culm diameter at breast height, $D_{ramet} \geq 2$ cm), *Gigantochloa ligulata* Gamble (1107 ramets ha^{-1}), and *Schizostachyum grande* Ridl. (556 ha^{-1}), to be the target species for this study. These species are endemic to the Malay Peninsula, and are commonly distributed in hill and upper hill forests (Wong 1995). *Gigantochloa ligulata* was the shortest among the four co-occurring bamboo species with 6–9-m-tall genet crowns, and *Schizostachyum grande* was the tallest bamboo in the study site with 9–15-m-tall crowns (Wong 1995). According to the monograph of Malaysian bamboos by Wong (1995), the two species commonly occur in disturbed areas with *G. ligulata* found from lowlands to hillsides, and *S. grande* more restricted to hillsides. *Schizostachyum grande* exhibits a monocarpic flowering pattern, a common property of bamboos, meanwhile *G. ligulata* exhibits continuous partial flowering among ramets in an individual genet. Neither of the species

Table 1. Notation list of architectural dimensions, biomass turnover attributes and stand scale properties.

Notation	Unit	Scale	Definition
A_{ramet}	m^2	ramet	Total leaf area of ramet
A_{genet}	m^2	genet	Total leaf area of genet: $\Sigma^n A_{ramet}$
A_{tree}	m^2	tree	Total leaf area of tree
B_{stand}	y^{-1}	stand	Instantaneous (not annualized) wood production rate per stand biomass
C_{genet}	m^2	genet	Area of leafy crown per genet
C_{tree}	m^2	tree	Area of leafy crown per tree
CLAI	$m^2\,m^{-2}$	genet	Leaf area index within a crown of genet or tree: A_{genet}/C_{genet} (A_{tree}/C_{tree})
D_{ramet}	cm	ramet	Culm diameter at breast height
D_{genet}	cm	genet	Mean diameter of ramets in genet
D_{tree}	cm	tree	Diameter of tree stem
H_{ramet}	m	ramet	Height of the highest leaf of ramet
H_{genet}	m	genet	Genet height of the highest leaf
H_{tree}	m	tree	Height of the highest leaf
k_{sample}		ramet	Number of internodes sampled
k_{total}		ramet	Number of internodes in culm
LAI	$m^2\,m^{-2}$	stand	Leaf area index: ΣA_{genet} (A_{tree}) / Q
LAI_{intact}	$m^2\,m^{-2}$	stand	LAI of canopy trees ($D_{tree} \geq 45$ cm) at before logging in 2008 (20 m by 40 m scale)
LAI_0	$m^2\,m^{-2}$	stand	LAI of canopy trees ($D_{tree} \geq 45$ cm) at the first census (20 m by 40 m scale)
LAI_{loss}	$m^2\,m^{-2}$	stand	LAI of trees which died during logging phase (2008 - 2011) (20 m by 40 m scale)
M_{stand}	y^{-1}	stand	Instantaneous wood loss rate per stand biomass
n		genet	Number of ramets per genet
P_i	kg or m^2	ramet	Architectural dimensions at internode i
P_{ramet}	kg or m^2	ramet	Ramet-scale dimensions
Q	ha or m^2	stand	Area of target plot
R_{stand}	y^{-1}	stand	Relative rate of stand biomass increase, as $B_{stand} - M_{stand}$
S_{genet}	cm^2	genet	Total basal area of consisting culms in genet
T	y		Census interval varied from 14 to 17 mo
Notation	Unit	Scale	Detail
W_{branch}	kg	ramet	Total branch weight of ramet or tree
W_{culm}	kg	ramet	Culm weight of ramet
W_{genet}	kg	genet	Above-ground weight of genet
W_j	kg	genet	Above-ground weight of individual genet (tree)
W_{leaf}	kg	ramet	Total leaf weight of ramet or tree
W_{ramet}	kg	ramet	Above-ground weight of ramet: $W_{ramet} = W_{culm} + W_{branch} + W_{leaf}$
W_{stand}	kg ha^{-1}	stand	Above-ground biomass of bamboo or tree
$W_{stand,\,0}$	kg ha^{-1}	stand	Above-ground biomass at the first census
$W_{stand,\,death}$	kg ha^{-1}	stand	Above-ground biomass of dead plants by the second census
$W_{stand,\,growth}$	kg ha^{-1}	stand	Above-ground biomass increment due to tree growth by the second census
$W_{stand,\,recruit}$	kg ha^{-1}	stand	Above-ground biomass of recruited plants by the second census
W_{stem}	kg	tree	Stem weight of tree
W_{tree}	kg	tree	Above-ground weight of tree: $W_{tree} = W_{stem} + W_{branch} + W_{leaf}$

showed synchronized flowering among genets during the course of our study.

Measurement of crown architecture

We sampled ramets of these two bamboo species outside the 24 plots in the study site (Appendix 1). Both species exhibited sympodial rhizome branching and formed distinct clumps consisting of multiple ramets that were closely packed at the ground level. We assumed that each visible clump of culms was an independent genet, though exceptions have been shown to exist for other clumping species (Franklin *et al.* 2008). We selected 29 and 25 genets of *G. ligulata* and *S. grande*, respectively,

with six to eight genets each in the following four size classes. In order to sample genets from a wide range of genet sizes, the genet size class was determined based on the observed frequency distributions of ramet number per genet (n) on a logarithmic scale in the permanent plots, where only ramets with culm diameter at breast height ≥ 2 cm (D_{ramet}) were counted. The size classes were 2–5, 6–15, 16–36 and 37–83 ramets per genet for *G. ligulata*, and 2–4, 5–9, 10–21 and 22–45 ramets for *S. grande*.

For each of the selected genets, we calculated the total basal area of all constituent ramets (S_{genet}, cm^2) and measured the top crown height (H_{genet}, m) with either a splice measurement pole up to 15 m (AT-15, Myzox) or an electronic hypsometer (VERTEX IV, Haglöf

Sweden AB, Långsele) (Appendix 2). We measured two perpendicular horizontal crown widths along the contour and slope directions, from which we obtained the area of leafy crown (C_{genet}, m^2) assuming ellipsoids (Appendix 2). From each selected genet, we measured the top height of a ramet (H_{ramet}, m) that had an intermediate diameter of the ramets in that genet, and then harvested the ramet from the base at ground level.

Since each internode of a culm is a modular unit bearing branches and leaves (McClure 1966, Pearson *et al.* 1994), we used internodes within a culm, including the lower node, as a sampling unit from which we estimated the architectural dimensions of a whole ramet. We sampled every other internode for *G. ligulata* and every fourth internode for *S. grande* (because *G. ligulata* showed more irregular branching on a culm than *S. grande*). We measured fresh weight of culm, branch and leaves in the field, and brought back partial subsamples of culm-stem and leaves (two from every sampled internode) from base to top of internode samples of every culm to the laboratory in FRIM. There they were oven dried at 80°C over 4 d and then weighed. We estimated the oven-dry weight of components of sampled internodes by applying the ratio of dry to fresh weight of subsamples (culm-stem ratio was used for culm stem and branch stem). We measured fresh leaf area of leaf subsamples using a photo scanner (LiDE 110, CANON, at 75 ppi) and image analysis software (Image J, NIH). We used the ratio of leaf area to fresh leaf weight of each sampled internode to estimate the total leaf area per internode. Finally, we estimated biomasses of culm (W_{culm}, kg), branch (W_{branch}, kg), and leaf (W_{leaf}, kg), and total leaf area (A_{ramet}, m^2) in each culm using sampled internodes with the equation:

$$P_{ramet} = [k_{total}/k_{sample}]\Sigma_i P_i \qquad (1)$$

where P_{ramet} is a ramet-scale dimension (biomass or area), k_{total} is the number of internodes in the culm, k_{sample} is the number of internodes sampled, and P_i is an internode-scale dimension of the *i*-th internode sample.

In the permanent plots, we measured the crown architecture of bamboos at the first census. To determine genet-scale top height (H_{genet}), total basal area of all culms (S_{genet}) and crown area (C_{genet}) (Appendix 2), we surveyed all genets in the central 10×30 m of the 24 plots (Appendix 3). In total, we obtained data from 97 genets for both *G. ligulata* and *S. grande*.

Bamboo allometries

We employed a set of allometric relationships to link architectural dimensions at the ramet-scale (D_{ramet}, W_{culm}, W_{branch}, W_{leaf} and A_{ramet}) and those at the genet-scale (n, S_{genet}, C_{genet} and H_{genet}) (Figure 1; Appendix 2). To
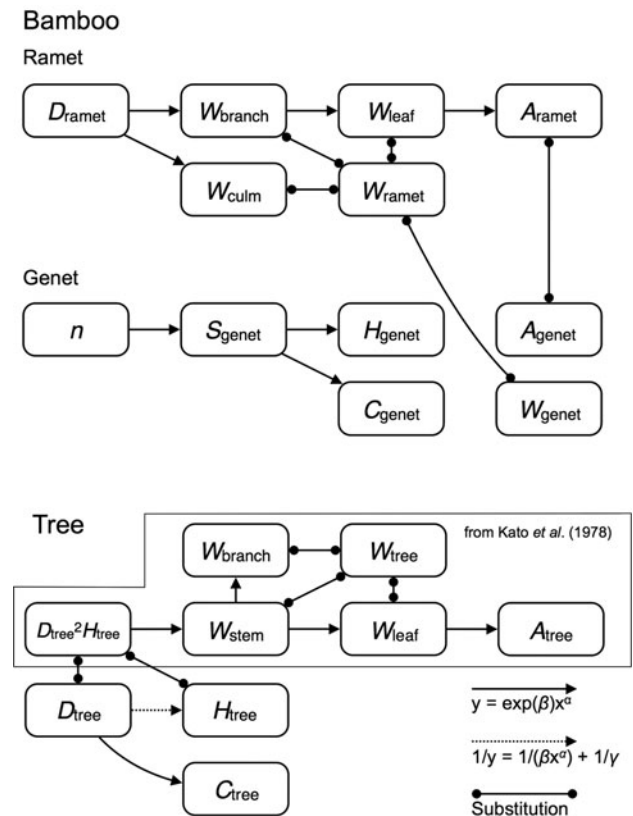

Figure 1. Allometric estimation for bamboo ramets, bamboo genets and woody trees in a Malaysian hill rain forest. The type of arrow indicates allometric equations that connect dimensions. Enclosed allometric equations for trees are by Kato *et al.* (1978) in Pasoh Nature Reserve. See Table 1 for the definition of the dimensions and Appendix 2 for observation scheme.

estimate allometric parameters of a *Y*-on-*X* allometry for bamboos, we employed power functions, $Y = \exp(\beta)X^\alpha$, where *X* and *Y* are architecture dimensions, α is a scaling exponent, and β is an allometric constant. As suggested by Wright *et al.* (2006), ordinary linear regression analysis is appropriate, when the purpose is to predict a dimension from another explanatory dimension. Therefore, we estimated α and β by fitting a log-linear fixed model, $\ln Y = \beta + \alpha \ln X$, with Type I regression, i.e. measurement errors are assigned on *Y* measures. We examined species differences in α or β by setting species identity as a fixed effect, and conducted model selection based on the corrected Akaike information criterion, AICc (Hurvich & Tsai 1989). This allowed us to examine whether (1) both α and β were different between species, (2) only β was species specific, or (3) both α and β were common across species. We estimated genet-scale dimensions of biomass (W_{genet}) and leaf area (A_{genet}) by applying the ramet-scale allometries to the observed D_{ramet} of all the constituent ramets of each genet (Figure 1).

Tree architecture and allometry

For woody trees, we measured stem diameter at breast height (D_{tree}, cm), tree height (H_{tree}, m) and the area of leafy crown (C_{tree}, m^2) for all individuals with $D_{tree} \geq 5$ cm in eight plots (1.28 ha) of the 24 permanent plots (20 × 80 m each; Appendices 1, 3) in 2008, using the same protocol for bamboos. We employed a hyperbolic function for H_{tree} on D_{tree} allometry ($1/H_{tree} = 1/(\beta D_{tree}{}^{\alpha}) + 1/\gamma$) and a power function for C_{tree} on D_{tree} allometry ($C_{tree} = \exp(\beta)D_{tree}{}^{\alpha}$) (Figure 1).

To calculate above-ground tree biomass, we employed the allometric equations of Kato *et al.* (1978) determined in the Pasoh Forest Reserve (2°60′N, 102°19′E), located 300 km south from the study site. These allometric equations are as follows (Figure 1):

$$W_{stem} = 0.0313(D_{tree}{}^2 H_{tree})^{0.9733} \qquad (2)$$

$$W_{branch} = 0.136 W_{stem}{}^{1.07} \qquad (3)$$

$$1/W_{leaf} = 1/(0.124\,W_{stem}{}^{0.794}) + 1/125, \text{ and} \quad (4)$$

$$A_{tree} = 11.4\,W_{leaf}{}^{0.900}, \qquad (5)$$

where W_{stem} is the stem dry mass (kg), and A_{tree} is the total leaf area of a tree (m^2). Above-ground biomass of tree was thus $W_{tree} = W_{stem} + W_{branch} + W_{leaf}$.

Allometry comparison

We compared predicted Y values at the reference values of X among the two bamboo species and woody trees in the two ramet-scale and six genet-scale allometries from the perspective of light capture efficiency, i.e. H_{ramet} (H_{tree}) on D_{ramet} (D_{tree}) and W_{culm} (W_{stem}), W_{branch}, A_{genet} (A_{tree}) and H_{genet} (H_{tree}) on W_{genet} (W_{tree}), and A_{genet} (A_{tree}), C_{genet} (C_{tree}) and CLAI on H_{genet} (H_{tree}). CLAI was calculated as A_{genet}/C_{genet} (A_{tree}/C_{tree}) (m^2 m^{-2}). To quantify the difference in predicted Y values between species, we chose three reference values of X (W_{genet}, W_{tree}, H_{genet} or H_{tree}), i.e. at the minimum and maximum points, and geometric midpoint across their range of overlap (Appendix 4).

Observation and estimation of biomass dynamics

By employing the architectural allometries, we estimated demographic turnover rates of stand-scale biomass of bamboos and trees. We first recorded the death and recruitment of bamboo ramets and tree stems and increment in stem diameter for trees for a subplot of 10 × 30 m for bamboos and 20 × 40 m for trees, in all the 24 plots (Appendix 3). The census intervals varied from 14 to 17 mo (first census was from February to July 2011, and the second census was from August to September 2012). For woody trees, we tagged stems with $D_{tree} \geq 5$ cm in the first census and recorded their survival, increase in diameter and recruitment to $D_{tree} \geq 5$ cm in the second census. We tagged and painted every culm of bamboo genets comprised of at least one ramet with $D_{ramet} \geq 2$ cm in the first census, and recorded dead and recruited ramets at the second census. To compare dynamics between bamboos and trees in the same light environment, we selected genets and trees located in the same layer of the forest canopy. Top height of trees (H_{tree}) predicted by the allometry from stem diameter (D_{tree}) at 5 cm was $H_{tree} = 6.7$ m, i.e. the lower boundary height of tree census, and the corresponding genet sizes were n = 4 for *G. ligulata* ($H_{genet} = 6.7$ m) and n = 3 for *S. grande* ($H_{genet} = 7.0$ m). Therefore, genets with ramets equal to or more than these thresholds were used for comparison. Similarly, we applied an upper boundary D_{tree} range to keep tree height within the height range of bamboo crowns. We employed $D_{tree} = 40.4$ cm corresponding to $H_{tree} = 27.3$ m, the maximum height observed in *S. grande*.

We estimated demographic turnover rates of above-ground biomass, based on the census records of D_{ramet} (or D_{tree}) and allometric equations that relate D_{ramet} (or D_{tree}) and biomass dimension, W_{ramet} (or W_{tree}). Above-ground biomass W_{stand} (kg ha^{-1}) was defined by $W_{stand} = [\Sigma_j W_j]/Q$, where W_j (kg) is biomass of the *j*-th individual genet (or tree) and Q (ha) is the area of a target plot (Appendix 3). To standardize time intervals, we employed the continuous-time model of the dynamics of above-ground biomass:

$$dW_{stand}/dt = R_{stand}W_{stand} = (B_{stand} - M_{stand})\,W_{stand}, \qquad (6)$$

where R_{stand} (y^{-1}) is the net specific rate of biomass increase, B_{stand} (y^{-1}) is the instantaneous (not annualized) specific wood production rate, M_{stand} (y^{-1}) is the instantaneous specific wood loss rate and t is census interval (y) (Kohyama *et al.* in press). By integrating Eq. 6 with respect to the duration from $t = 0$ to T, we obtain estimates of R_{stand}, M_{stand} and B_{stand} as (Phillips *et al.* 1994),

$$R_{stand} = \big[\ln(W_{stand,0} - W_{stand,death} + W_{stand,growth}$$
$$+ W_{stand,recruit}) - \ln(W_{stand,0})\big]/T, \qquad (7)$$

$$M_{stand} = \big[\ln(W_{stand,0}) - \ln(W_{stand,0}$$
$$- W_{stand,death})\big]/T, \text{ and} \qquad (8)$$

$$B_{stand} = [\ln(W_{stand,0} - W_{stand,death} + W_{stand,growth}$$
$$+ W_{stand,recruit}) - \ln\big(W_{stand,0} - W_{stand,death}\big)\,]/T, \qquad (9)$$

where $W_{stand,0}$ (kg ha^{-1}) is living biomass at the first census, $W_{stand,death}$ (kg ha^{-1}) is a portion of $W_{stand,0}$ that

Table 2. Estimated allometric parameters for two bamboo species: Gl for *Gigantochloa ligulata* and Sg for *Schizostachyum grande*. The estimated scaling exponents (α) and allometric constants (β) between two dimensions X and Y, $Y = \alpha \ln X + \beta$, are shown for 95% confidence interval. Refer to Figure 1 for the form of equations. R^2 is the coefficient of determination of the models. Type 1 represents two bamboo species shared common α and β; Type 2 represents difference between the two species only in β; and Type 3 represents difference between the two species in α (therefore, also in β). Parameters identical between the two species are showed only for *G. ligulata*. P-values of all the estimated α were less than 0.001.

	X	Y	Sp.	α 2.5%	mean	97.5%	β 2.5%	mean	97.5%	R^2	Type
Ramet	D_{ramet} (cm)	H_{ramet} (m)	Gl	0.496	0.801	1.11	0.511	0.937	1.36	0.336	1
			Sg								
G. ligulata (29)	D_{ramet} (cm)	W_{culm} (kg)	Gl	2.37	2.70	3.02	−3.70	−3.24	−2.79	0.838	1
S. grande (25)			Sg								
	D_{ramet} (cm)	W_{branch} (kg)	Gl	1.29	2.11	2.93	−3.86	−2.82	−1.78	0.328	2
			Sg				−3.81	−3.26	−2.70		
	W_{branch} (kg)	W_{leaf} (kg)	Gl	0.606	0.744	0.881	−1.25	−1.05	−0.846	0.699	2
			Sg				−1.14	−0.840	−0.545		
	W_{leaf} (kg)	A_{ramet} (m²)	Gl	1.00	1.04	1.07	2.89	2.95	3.01	0.987	2
			Sg				2.94	3.00	3.07		
Genet	n	S_{genet} (cm²)	Gl	1.09	1.18	1.27	1.6	1.82	2.05	0.906	3
			Sg	2.66	1.57	2.84	1.35	1.64	1.92		
G. ligulata (97)	S_{genet} (cm²)	C_{genet} (m²)	Gl	0.501	0.612	0.724	0.39	0.904	1.42	0.733	3
S. grande (97)			Sg	1.38	0.849	1.54	−0.398	0.234	0.866		
	S_{genet} (cm²)	H_{genet} (m)	Gl	0.118	0.173	0.227	1.05	1.30	1.55	0.513	3
			Sg	0.461	0.329	0.541	0.531	0.841	1.15		

was lost by death, $W_{stand, growth}$ (kg ha^{-1}) is biomass increment due to tree growth during the census period (and is assumed zero for bamboo ramets), and $W_{stand, recruit}$ (kg ha^{-1}) is the biomass increment due to newly recruited plants at the second census, and T (y) is census interval. Permanent plots in which a whole $W_{stand, 0}$ was lost during two censuses were excluded from the following analysis. Likewise, plots in which $W_{stand, 0}$ was zero were excluded from the analysis.

Response of biomass dynamics to canopy disturbance

We compared effects of the forest canopy conditions on biomass density, $W_{stand, 0}$, and on the specific rate of biomass increase, R_{stand}, for trees and bamboos as follows. Canopy conditions were evaluated by canopy LAI (m^2 m^{-2}) before logging in 2008 (LAI$_{intact}$), the first census (LAI$_0$), and by the loss of canopy LAI (LAI$_{loss}$) between 2008 to 2011 (as logging took place in 2010). Canopy LAI was calculated for the trees with $D_{tree} \geq 45$ cm, which is the maximum size of trees protected from logging operations under the Selective Management System (SMS) of Malaysian forestry practice. This threshold of D_{tree} for canopy trees was significantly larger than the subset of plants for biomass dynamics that was $D_{tree} \leq 40.4$ cm as stated above. We developed linear regression models to examine the effects of LAI$_{intact}$ on $W_{stand, 0}$ and effects of LAI$_0$ and LAI$_{loss}$ on R_{stand}, separately for woody trees, *G. ligulata* and *S. grande*, with the model selection based on AICc (Hurvich & Tsai 1989). We carried out these analyses using R 3.3.3 (R Core Team, https://www.R-project.org/) with the package MuMIn for AICc calculation (https://CRAN.R-project.org/package=MuMIn) and raster and ggplot2 for mapping the study site (Appendix 1).

RESULTS

Allometric properties

The observed maximum ramet number per genet of *G. ligulata* and *S. grande* was 110 and 45, respectively. The mean and maximum diameters of all observed ramets were 3.7 cm and 7.6 cm for *G. ligulata*, and 5.5 cm and 10.3 cm for *S. grande*, respectively. The maximum crown height among all observed genets was 17.5 m for *G. ligulata* and 27.3 m for *S. grande*. The maximum stem diameter at breast height of woody trees was 182 cm and the maximum height was 49.4 m. The estimated parameters of the allometric equations used are given in Table 2 (bamboos) and Table 3 (trees).

Compared with tree stems, both ramets and genets of the two bamboo species had more efficient crown architectures in terms of biomass expenditure for displaying leaves. Culms of *S. grande* attained 1.3 times more height than woody tree stems at a diameter of 6.6 cm (Figure 2a). This value of 6.6 cm corresponds to the geometric midpoint of the range of the observed diameter distribution (Appendix 4). On the basis of culm (stem) biomass, there were similar contrasts between the top height of bamboo culms and tree stems, where both *G. ligulata* and *S. grande* culms were 1.5 times as tall

Table 3. Estimated allometric parameters for trees. N represents the number of samples. The mean estimated coefficients of α, β, and γ along with confidence intervals are given for equations estimating height (H_{tree}) and canopy area (C_{tree}) as a function of stem diameter (D_{tree}): $1/Y = 1/(\beta X^{\alpha}) + 1/\gamma$. R^2 is the coefficient of determination of the models. P-values of all the estimated parameters were less than 0.001.

X	Y	N	α 2.50%	mean	97.50%	β 2.50%	mean	97.50%	γ 2.50%	mean	97.50%	R^2
D_{tree} (cm)	H_{tree} (m)	899	0792	0.889	0.991	1.52	1.80	2.10	49.1	63.0	92.7	0.754
D_{tree} (cm)	C_{tree} (m²)	813	118	1.25	1.32	−0.764	−0.58	−0.397				0.590
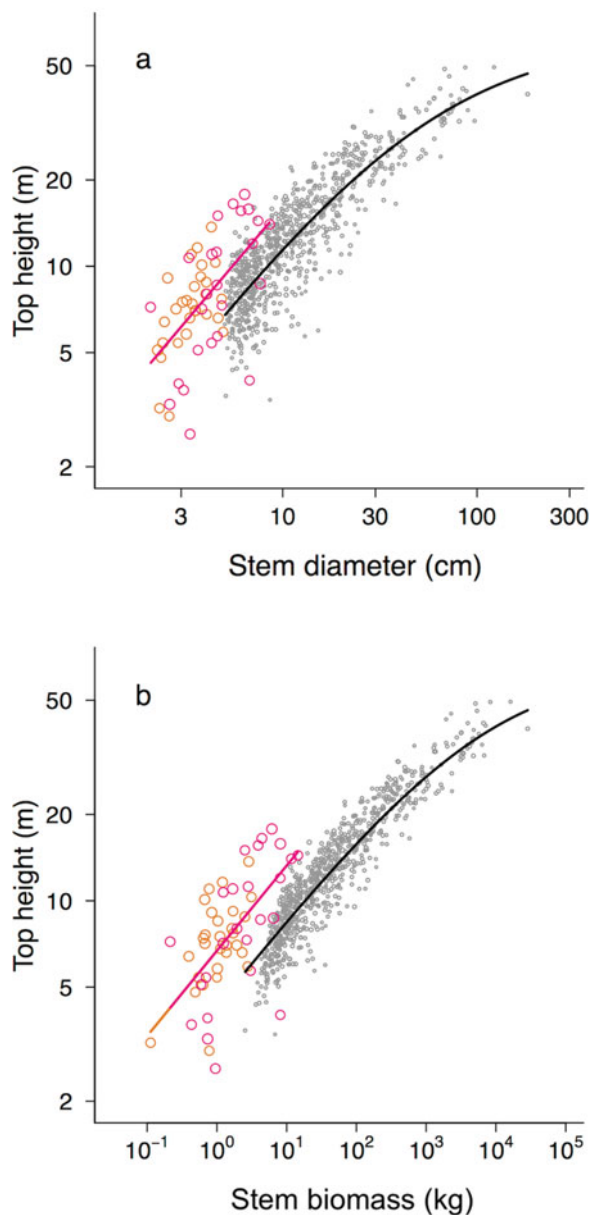
Figure 2. Allometric properties of bamboo ramets and woody trees in a Malaysian hill rain forest. Ramet (stem) top height (H_{ramet}, H_{tree}) on culm (stem) diameter at breast height (D_{culm}, D_{tree}) (a) and on culm (stem) biomass (W_{culm}, W_{stem}) (b) for *Gigantochloa ligulata* (orange), *Schizostachyum grande* (pink) and woody trees (grey). Solid lines show the allometric predictions.

(Figure 2b). The bamboo culms were on average taller than trees, even though some of their culms were slanted or bent (Appendix 2), which would also contribute to the large variation in height at a given culm diameter or biomass. At the genet-scale comparison, *G. ligulata* and *S. grande* allocated 2.7 and 1.8 times more in lateral branch biomass, and supported 4.4 and 4.2 times larger leaf area, than trees, respectively (Figure 3a-b), at an above-ground biomass of 30 kg for *G. ligulata* genets vs. trees and an above-ground biomass of 50 kg for *S. grande* genets vs. trees. With respect to crown height at the geometric midpoints of above-ground biomass, trees on average had an intermediate height between *G. ligulata* and *S. grande*. These bamboos attained heights of 0.79 and 1.1 times that of trees, respectively (Figure 3c).

At reference crown heights of 7.7 m for *G. ligulata* and 9.7 m for *S. grande*, bamboos displayed 5.9 and 3.0 times more total leaf area, and 6.6 and 6.7 times larger crown projection area than trees of the same crown height, respectively (Figure 5a-b). As a consequence of more leaves in the larger crown area, *G. ligulata* and *S. grande* constructed crowns of similar or lower density at reference heights, resulting in crown leaf area indices that were 10% and 55% lower than trees, respectively (Figure 5c).

Between the two bamboo species, ramet-scale allometry of top height on culm diameter and that on culm biomass were not significantly different (Figure 2a-b, Table 2). At the genet-scale, *G. ligulata* allocated 1.4 times as much above-ground biomass to lateral branches as *S. grande* (Figure 3a). Accordingly, the height of the genet crown of *G. ligulata* was 20% shorter than that of *S. grande* at 14 kg above-ground biomass (Figure 3c), which was partly attributable to the fact that *G. ligulata* genets consisted of a larger number of smaller ramets as compared with a *S. grande* genet at the same above-ground biomass (Figure 4). Despite the difference in biomass allocation to lateral branches between the two bamboos, total leaf area at the same above-ground biomass was similar (1.1 times as large in *G. ligulata* as in *S. grande*) (Figure 3b). At the geometric midpoint of the measured crown height range for both bamboos (7.1 m), *G. ligulata* displayed 1.7 times as much leaf area as did *S. grande* (Figure 5a), while crown area of the two bamboos did not show a large difference (10% larger in *G. ligulata*) (Figure 5b). Therefore, CLAI of *G. ligulata* was 1.5 times that of *S. grande* at the reference
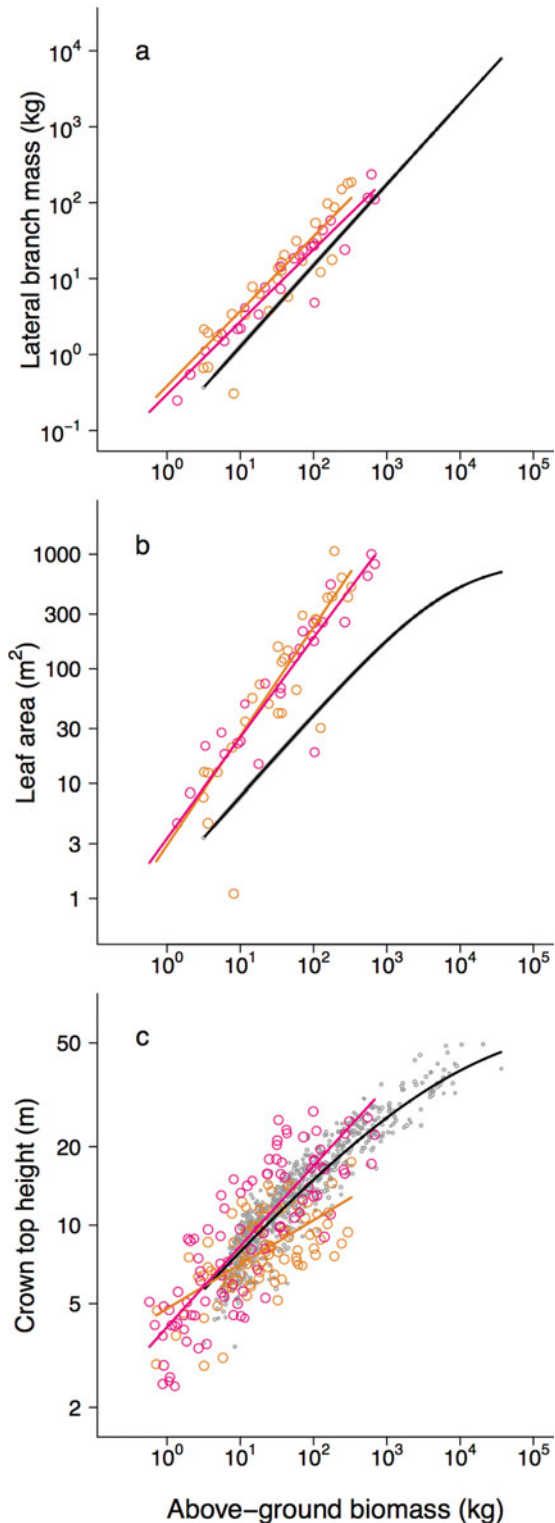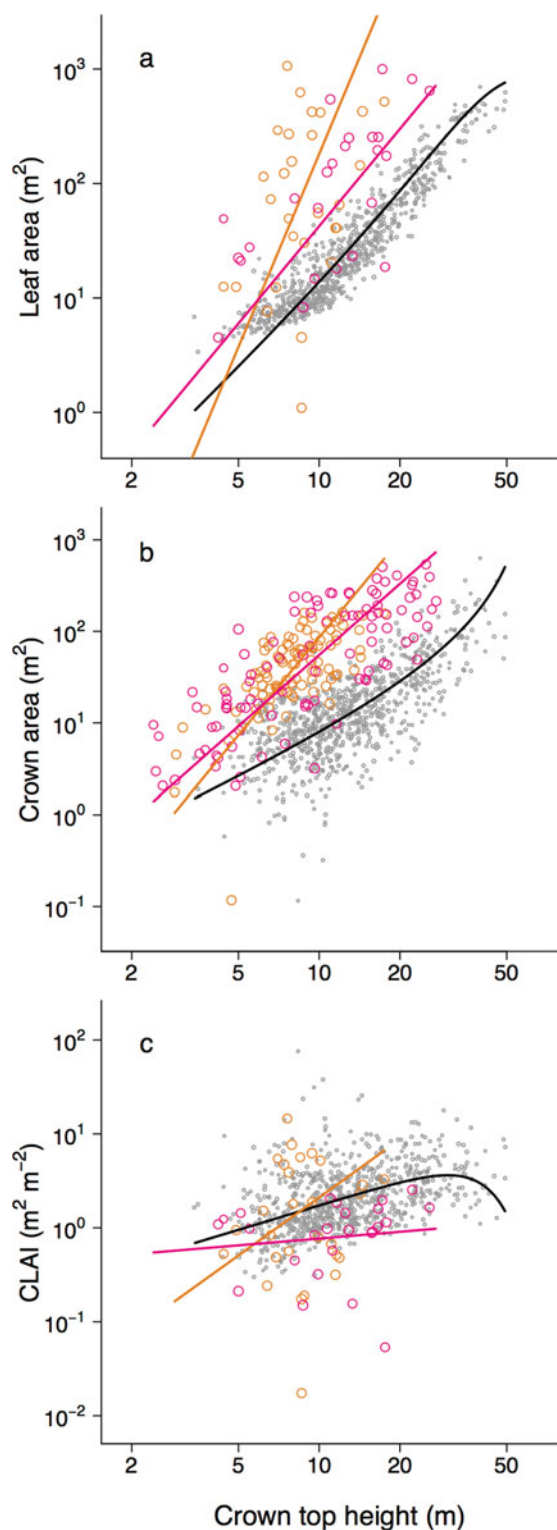
Figure 3. Allometric properties relative to above-ground biomass (W_{genet}, W_{tree}) for genets and stems in a Malaysian hill rain forest; *Gigantochloa ligulata* (orange), *Schizostachyum grande* (pink) and woody trees (grey). Solid lines show the allometric predictions. Allometric relation with branch biomass (W_{branch}) (a), leaf area (A_{genet}, A_{tree}) and crown top height (H_{genet}, H_{tree}) (c).

height, although variation in predicted CLAI was large (Figure 5c).

Population and biomass dynamics

In the 2011 census of 24 permanent plots after the logging experiment, there were 2023 ramets and 132 genets of *G. ligulata* with the number of ramets $n \geq 4$, and 982 ramets and 130 genets of *S. grande* with $n \geq 3$. In these subplots, there were 1508 stems of trees including 67 canopy trees (stem diameter $D_{tree} \geq 45$ cm) and 1424 stems of middle-canopy trees sharing the subcanopy layer with bamboos ($D_{tree} \leq 40.4$ cm).

Above-ground biomass of trees was 341 Mg ha^{-1}, and that for *G. ligulata* and *S. grande* was 3.3 and 4.0 Mg ha^{-1}, respectively. In contrast to the 100-fold difference in biomass, stand-level LAI was 4.38, 0.68 and 0.52, for trees, *G. ligulata* and *S. grande*, respectively. Demographic turnover rate of biomass for bamboo ramets was 4.5 times or more that of woody trees in the subcanopy layer (Figure 6, Appendix 5). The average of estimated instantaneous specific wood loss rate (M_{stand}) was 0.16, 0.22 and 0.033 y^{-1} for *G. ligulata*, *S. grande* and trees, respectively, whereas instantaneous specific wood production rate (B_{stand}) was 0.27, 0.43 and 0.057 y^{-1} for *G. ligulata*, *S. grande* and trees, respectively (Appendix 5). Therefore, average rate of net specific biomass increase ($R_{stand} = B_{stand} - M_{stand}$) was +0.11, +0.27 and +0.024 y^{-1} for *G. ligulata*, *S. grande* and trees, respectively (Appendix 5).

The second census of the 24 subplots showed decreasing mean stand LAI from pre-logging conditions in 2008 of 1.70 m^2 m^{-2} (LAI$_{intact}$) to post-logging conditions in 2011 of 1.42 m^2 m^{-2} (LAI$_0$), where lost LAI due to logging (LAI$_{loss}$) varied from 0 to 3.76 m^2 m^{-2} among the plots (Appendix 6). Stand biomass ($W_{stand, 0}$) for *G. ligulata* showed a negative correlation with LAI$_{intact}$ ($R^2 = 0.313$), while that of *S. grande* and subcanopy trees had no correlation with LAI$_{intact}$ (Table 4). Net specific rate of biomass increase (R_{stand}) of *G. ligulata* during the census period showed a positive correlation with LAI$_{loss}$ ($R^2 = 0.548$), while that of *S. grande* did not correlate with either LAI$_0$ or LAI$_{loss}$ (Figure 6). In contrast to *G. ligulata*, R_{stand} of subcanopy trees was negatively correlated with LAI$_{loss}$ (Figure 6) ($R^2 = 0.251$).

DISCUSSION

To understand why tropical bamboos persist in mature forest stands and recover vigorously after disturbance, we proposed the hypothesis that the architecture of bamboos is more efficient for light capture than that of woody trees, and tested this hypothesis by examining the architectural
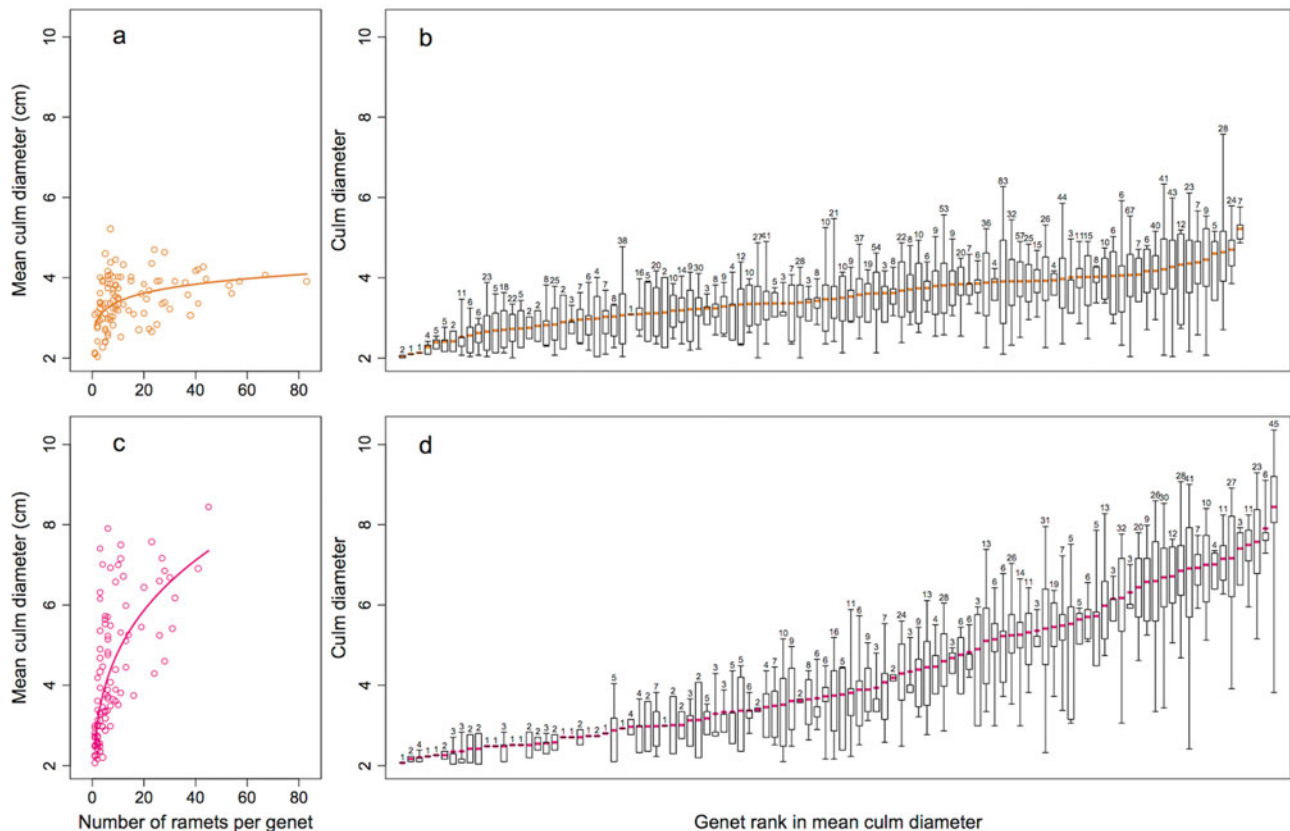
Figure 4. Distribution of culm diameter (D_{ramet}) in genets of *Gigantochloa ligulata* (a, b) and *Schizostachyum grande* (c, d) in a Malaysian hill rain-forest. Left panels (a, c): average D_{ramet} per genet (D_{genet}) vs. number of ramets per genet (n). Right panels (b, d): change in D_{ramet} distribution per genet along the genet rank in D_{genet}. The lower and upper limits of the box plot in right panels represent 25- and 75-percentile D_{ramet}, respectively, and midpoint bar of each box shows D_{genet}. Whiskers represent the minimum and the maximum D_{ramet}. Inset numbers indicate n.

and dynamic properties of bamboos in comparison with trees. Observation of the two most abundant bamboo species, *Gigantochloa ligulata* and *Schizostachyum grande*, revealed that, as compared with woody trees, hollow culms have greater height attainment per ramet and greater total leaf area per genet, as the less costly hollow stems allowed for higher biomass allocation to branches resulting in a larger crown projection area. Bamboos exhibited higher biomass turnover rates of ramet culms than tree stems. Taken together these findings suggest how bamboos respond to environmental change. This inference was also supported by our results that *G. ligulata* increased biomass in response to canopy removal by disturbance.

In our study, the specific rate of biomass increase to above-ground biomass was based on recruitment rates of ramet culms and tree stems, and radial growth rate of tree stems (but not for bamboos). To fully evaluate net primary production rate (NPP) of above-ground biomass, we further need to account for the fine-litter production rate (Clark *et al.* 2001). The rate of fine-litter production is defined as the rate of branch and leaf fall from living plants. Clark *et al.* (2001) compiled the ratio of annual

rates of litterfall to above-ground biomass in 39 tropical forests (average 0.032 ± 0.021 y^{-1}). Specifically, for the Pasoh Forest Reserve in Peninsular Malaysia they found the ratio of 0.025 y^{-1} (see also Kira 1978). Therefore, the specific biomass increment rate of bamboos (0.27 and 0.43 y^{-1} for *G. ligulata* and *S. grande*, respectively) is three to five times higher than the estimate for trees 5.0–40.4-cm in dbh (0.082 y^{-1}, Appendix 5). The difference in above-ground NPP between bamboos and trees would be even larger if the leaf fall from bamboo ramets was taken into account. Moreover, by including trees in the canopy layer (dbh > 40.4 cm), which consist of the dominant portion of above-ground biomass, specific NPP to above-ground biomass would be far smaller for trees than for bamboos.

Despite the marked difference in architecture and dynamics between bamboos and woody trees, the key features relevant to light capture were similar, such as crown height and crown LAI at the genet scale (Figure 3c, 5c). In the case of woody trees, constraints of mechanics and hydraulic requirements of stems and branches limit the amount of foliage and crown height that can be sustained by a stem of specified basal area (Niklas 2007).

Figure 5. Allometric properties relative to top crown height (H_{genet}, H_{tree}) for genets and stems in a Malaysian hill rain forest: *Gigantochloa ligulata* (orange), *Schizostachyum grande* (pink) and woody trees (grey). Solid lines show the allometric predictions. Allometric relation with leaf area (A_{genet}, A_{tree}) (a), crown area (C_{genet}, C_{tree}) (b), and crown LAI (CLAI) (c).

A bamboo ramet is composed of a culm and branches with hollow interior and thus has a large sapwood area per unit basal area (McClure 1966, Wong 1995), which enables them to maintain substantial amount of foliage per unit above-ground biomass. Furthermore, the hollow interior efficiently reduces culm biomass without compromising physical strength, and this allows bamboo ramets to allocate larger biomass to lateral branches and attain 1.5 times the height of woody trees at the same above-ground biomass. Therefore, the separation of biomass into numerous culms within a genet, although it does not contribute to height gain, is compensated for by the cheap ramet architecture for bamboos, and which results in similar above-ground biomass for height gain between bamboo genets and woody trees.

Even on the basis of culm/stem diameter, the top height of ramets, in particular of *S. grande*, was still higher than woody trees, though this is not readily explained by the efficiency of hollow culms. From a wood mechanical perspective, loadable weight and height that meet buckling safety limits should decrease with decreasing stem diameter (King *et al.* 2009, McMahon 1973). The observed higher allocation to lateral branches on thin culms should thus increase the risk of mechanical failure. However, the clumping genet structure of these bamboos, where adjacent ramet crowns may press against each other or intertwine their branches, could enable them to exceed the stability limits for a single stem. In addition, the extreme slenderness of the culms allows them to bend their tops to the ground without breaking, as is the case for slender-stemmed shrubs (Larjavaara 2015). Outward bending by ramets could benefit the genet by increasing its crown area and shading adjacent saplings of trees. Furthermore, the quick replacement of short-lived ramets should reduce the deleterious effects of any breakage due to mechanical instability and/or falling tree branches.

Bamboo genets successfully expanded their crowns by a larger amount of branches (Figure 3b), which is an architectural strategy that places higher importance of the light capture at a current light availability, instead of the investment in height gain to get better light availability (King 1990, Kohyama 1987, Kohyama & Hotta 1990, Yamada *et al.* 2000). As a consequence, the bamboos exhibited crown LAI in a similar range to that of woody trees, indicating that from the perspective of the architecture the two bamboo species possess shade tolerance to the extent of the average of the woody tree community.

Although bamboos exhibited efficient architectures, this does not assure their persistence as a species in tropical rain forest. The mechanism of plant species coexistence in forests has been partly explained by the separation of successional niches under a horizontally heterogeneous canopy structure (Rees *et al.* 2001). Along

Table 4. Coefficients of the best models from the analyses of the effects of canopy structure on $W_{\text{stand, 0}}$ and R_{stand}. Refer to Appendix 5 for the focal sizes of D_{tree} and n for response variables. R^2 is the coefficient of determination of the models.

Species	Response		Intercept	$\text{LAI}_{\text{intact}}$	LAI_0	LAI_{loss}	R^2
G. ligulata	$W_{\text{stand, 0}}$	$\ln(\text{kg ha}^{-1})$	9.10	-0.562			0.313
S. grande			7.74				0.000
Trees			11.3				0.000
G. ligulata	R_{stand}	y^{-1}	-0.0291			0.513	0.548
S. grande			0.268				0.000
Trees			0.0544			-0.0388	0.251
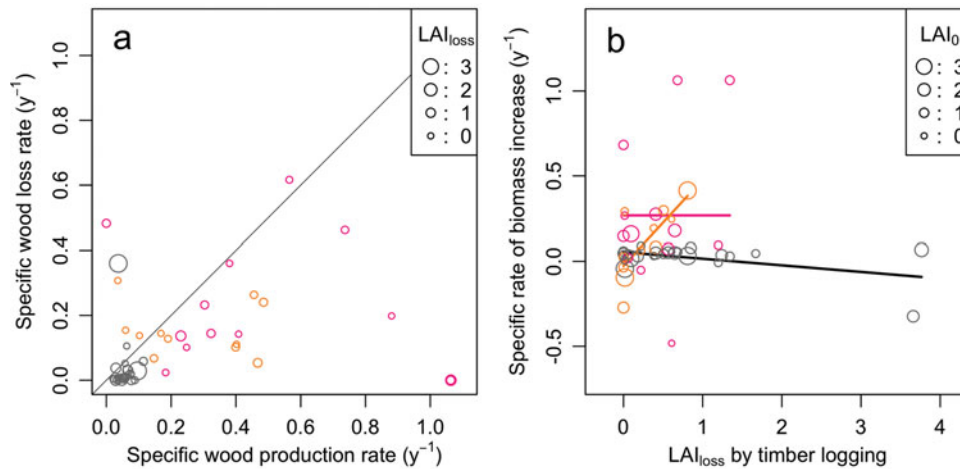
Figure 6. Demographic dynamic rates of above-ground biomass for *Gigantochloa ligulata* (orange), *Schizostachyum grande* (pink) and woody trees (grey) in a Malaysian hill rain forest (a); symbol size represents the degree of LAI loss by timber logging (LAI_{loss}) at each study plot. The relation between LAI_{loss} and net specific rate of biomass increase (coarse wood production rate relative to above-ground biomass), R_{stand} (b). Solid lines show predictions by selected empirical models in Table 4, where symbol size represents the LAI at the first census (LAI_0).

the spectrum of pioneer to climax species, bamboos might appear to be pioneers, as they exhibit quick recovery after forest disturbance. However, a number of typical properties of pioneer species (Swaine & Whitmore 1988) are not congruent with that of bamboos, and thus, the mechanism of bamboo persistence in the rain forest is not readily obvious in the context of successional niche theory. Kohyama & Takada (2009, 2012) developed another theory of species coexistence under the presence of one-sided competition for light along vertical foliage distribution, where demographic advantages permit the persistence of lower-canopy species without the aid of gap dynamics. As a clonal plant, which is known to be robust in species competition (Svensson *et al.* 2005, van Groenendael *et al.* 1996), shading (van Groenendael *et al.* 1996) and resource fluctuations (Suzuki & Stuefer 1999), a genet of bamboos is expected to maintain lower genet mortality under a forest canopy. As indicated by the wide crown architecture, bamboos also possess a certain degree of shade tolerance. These demographic advantages of bamboos fulfil conditions required for the coexistence with taller tree species in vertically stratified forest canopy (Kohyama & Takada 2009). Furthermore,

with their unique crown structure, bamboos possibly differentiate the vertical distribution of foliage in a life-form-specific manner distinguished from that of co-occurring tree species, and this provides a possibility of coexistence with similar-statured species as predicted by foliage partitioning theory (Kohyama & Takada 2012).

To understand how bamboos persist in a wide range of light conditions, previous studies suggested the importance of high photosynthetic plasticity of bamboo leaves in response to light (Montti *et al.* 2014, Yang *et al.* 2014). The present study sheds new insights on the uniqueness of bamboo architecture and its biomass dynamics. Instead of having large single stems like subcanopy tree species, the life-form of bamboos, which descended as a subfamily of Poaceae, is characterized by that of typical perennial grasses, with modular architecture, absence of cambial growth, and large subsidies of ramet recruitment from the rest of genet. Trees typically change their architecture by additions to their existing crowns, which are limited by relatively slow cambial growth in stems and branches. Hence they have a limited capacity to respond to rapid environmental change. This explains our observation that trees showed a decline in coarse

KING, D. A., DAVIES, S. J., TAN, S. & NUR SUPARDI, M. N. 2009. Trees approach gravitational limits to height in tall lowland forests of Malaysia. *Functional Ecology* 23:284–291.

KIRA, T. 1978. Community architecture and organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest, West Malaysia. Pp. 561–590 in Tomlinson, P. B. & Zimmermann, M. H. (eds.). *Tropical trees as living systems.* Cambridge University Press, Cambridge.

KLEINHENZ, V. & MIDMORE, D.J. 2001. Aspects of bamboo agronomy. *Advances in Agronomy* 74:99–153.

KOHYAMA, T. 1987. Significance of architecture and allometry in saplings. *Functional Ecology* 1:399–404.

KOHYAMA, T. & HOTTA, M. 1990. Significance of allometry in tropical saplings. *Functional Ecology* 4:515–521.

KOHYAMA, T. S., KOHYAMA, T. I. & SHEIL, D. in press. Definition and estimation of vital rates from repeated censuses: choices, comparisons and bias corrections focusing on trees. *Methods in Ecology and Evolution.*

KOHYAMA, T. & TAKADA, T. 2009. The stratification theory for plant coexistence promoted by one-sided competition. *Journal of Ecology* 97:463–471.

KOHYAMA, T. S. & TAKADA, T. 2012. One-sided competition for light promotes coexistence of forest trees that share the same adult height. *Journal of Ecology* 100:1501–1511.

LARJAVAARA, M. 2015. Trees and shrubs differ biomechanically. *Trends in Ecology and Evolution* 30:499–500.

MCCLURE, F. A. 1966. *The bamboos – a fresh perspective.* Harvard University Press, Cambridge. 347 pp.

MCMAHON, T. 1973. Size and shape in biology. *Science* 179:1201–1204.

MONTTI, L., VILLAGRA, M., CAMPANELLO, P. I., GATTI, M. G. & GOLDSTEIN, G. 2014. Functional traits enhance invasiveness of bamboos over co-occurring tree saplings in the semideciduous Atlantic forest. *Acta Oecologica* 54:36–44.

NIKLAS, K. J. 2007. Maximum plant height and the biophysical factors that limit it. *Tree Physiology* 27:433–440.

PEARSON, A. K., PEARSON, O. P. & GOMEZ, I. A. 1994. Biology of the bamboo *Chusquea culeou* (Poaceae: Bambusoideae) in southern Argentina. *Vegetatio* 111:93–126.

PHILLIPS, O. L., HALL, P., GENTRY, A. H., SAWYER, S. A. & VÁSQUEZ, R. 1994. Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Sciences USA* 91:2805–2809.

REES, M., CONDIT, R., CRAWLEY, M., PACALA, S. & TILMAN, D. 2001. Long-term studies of vegetation dynamics. *Science* 293:650–655.

SAHA, S., HOLBROOK, N. M., MONTTI, L., GOLDSTEIN, G. & CARDINOT, G. K. 2009. Water relations of *Chusquea ramosissima* and *Merostachys claussenii* in Iguazu National Park, Argentina. *Plant Physiology* 149:1992–1999.

SMITH, M. & NELSON, B. W. 2011. Fire favours expansion of bamboo-dominated forests in the south-west Amazon. *Journal of Tropical Ecology* 27:59–64.

SODERSTROM, T. R. & CALDERON, C. E. 1979. A commentary on the bamboos (Poaceae: Bambusoideae). *Biotropica* 11:161–172.

SUZUKI, J. & STUEFER, J. F. 1999. On the ecological and evolutionary significance of storage in clonal plants. *Plant Species Biology* 14:11–17.

SVENSSON, B. M., RYDIN, H. & CARLSSON, B. Å. 2005. Clonal plants in the community. Pp. 129–146 in van der Maarel, E. (ed.). *Vegetation ecology.* Blackwell Science, Oxford.

SWAINE, M. D. & WHITMORE, T. C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81–86.

TANG, Y., KACHI, N., FURUKAWA, A. & AWANG, M. 1999. Heterogeneity of light availability and its effects on simulated carbon gain of tree leaves in a small gap and the understory in a tropical rain forest. *Biotropica* 31:268–278.

VAN GROENENDAEL, J. M., KLIMEŠ, L., KLIMEŠOVÁ, J. & HENDRIKS, R. J. J. 1996. Comparative ecology of clonal plants. *Philosophical Transactions of the Royal Society B: Biological Sciences* 351:1331–1339.

WIDMER, Y. 1998. Pattern and performance of understory bamboos (*Chusquea* spp.) under different canopy closures in old-growth oak forests in Costa Rica. *Biotropica* 30:400–415.

WONG, K. M. 1995. *The bamboos of Peninsular Malaysia.* Forest Research Institute Malaysia, Kuala Lumpur. 200 pp.

WRIGHT, I. J., FALSTER, D. S. & WESTOBY, M. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews* 81:259–291.

YAMADA, T., YAMAKURA, T. & LEE, H. S. 2000. Architectural and allometric differences among *Scaphium* species are related to microhabitat preferences. *Functional Ecology* 14:731–737.

YANG, S., SUN, M., ZHANG, Y., COCHARD, H. & CAO, K. 2014. Strong leaf morphological, anatomical, and physiological responses of a subtropical woody bamboo (*Sinarundinaria nitida*) to contrasting light environments. *Plant Ecology* 215:97–109.

YAP, S. K. 2010. *Forest management and stump-to-forest gate chain-of-custody certification re-evaluation report for the: Perak Integrated Timber Complex (Perak ITC).* Scientific Certification Systems. Emeryville, Canada. 51 pp.

ZHANG, J. & CAO, M. 1995. Tropical forest vegetation of Xishuang-banna, SW China and its secondary changes, with special reference to some problems in local nature conservation. *Biological Conservation* 73:229–238.
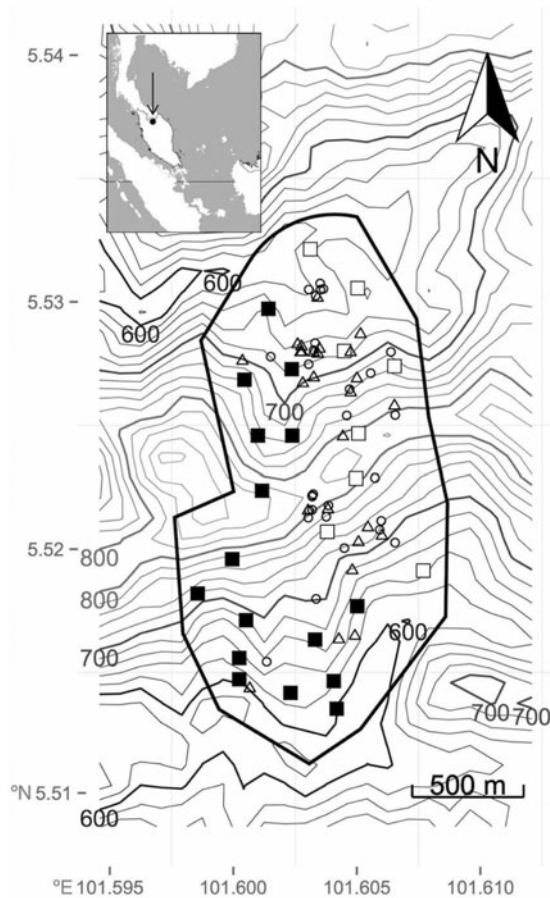
Appendix 1. Map of study site with 20-m contour lines. The thick border line traces the boundary of the study site (200 ha). Square symbols represent the location of 24 permanent plots, among which open squares indicate plots where tree crown architecture was observed. Circle and triangle symbols represent locations of *Gigantochloa ligulata* and *Schizostachyum grande* genets sampled for allometric analysis, respectively. For the destructive sampling, we searched genets in target size classes along logging trails by paying approximately equal efforts to the southern and northern slopes of the study site. Canopy condition above sampled genets were classified into three categories optically: closed canopy (C), intermediate (I) and open canopy (O). The numbers of sampled genets at each canopy condition (C, I and P) were 11, 9 and 9 for *G. ligulata*, and 9, 8 and 8 for *S. grande*, respectively.
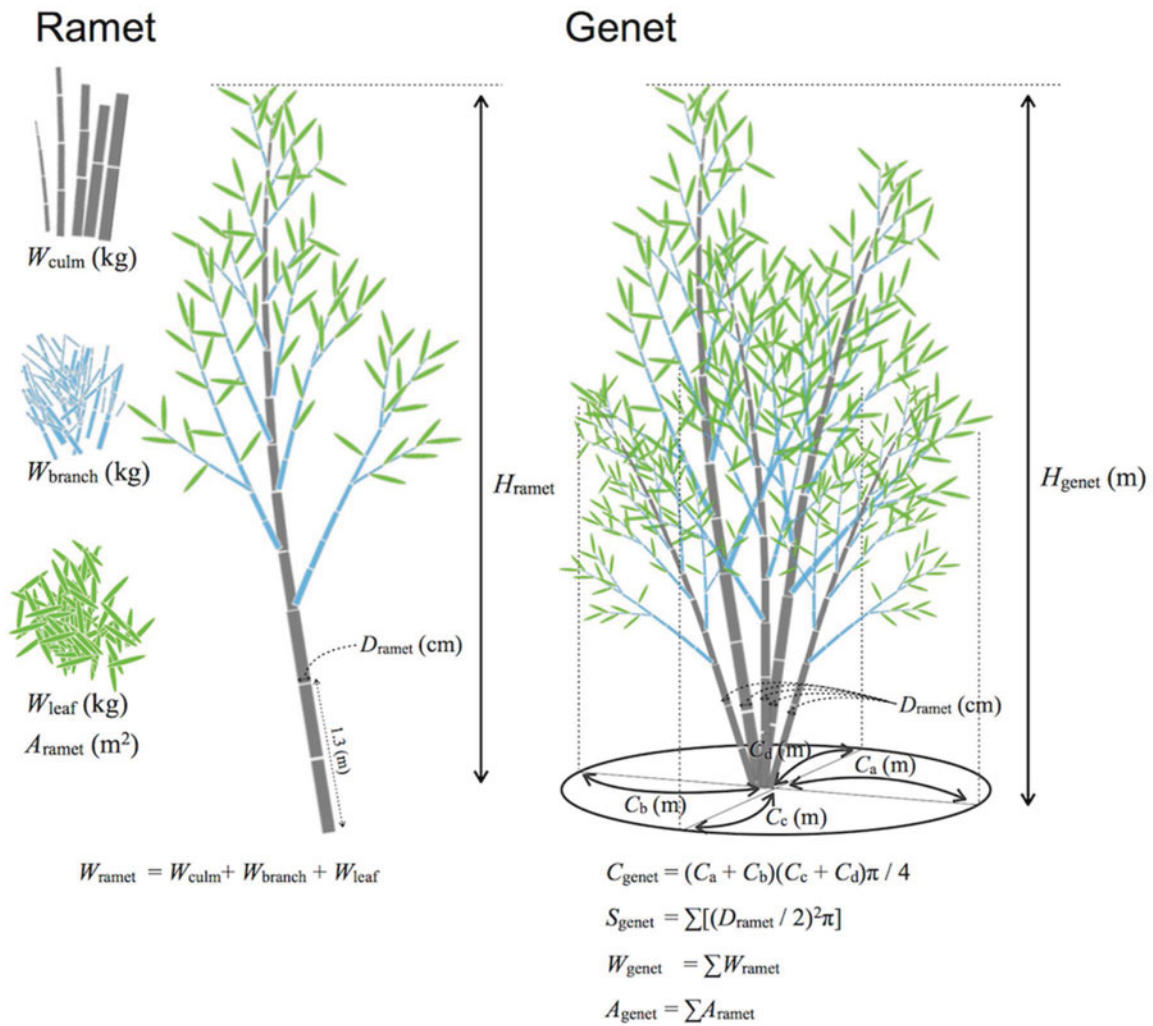
Appendix 2. Scheme of architectural observation and estimation for a bamboo ramet and genet. Above-ground biomass and total leaf area of genets, W_{genet} and A_{genet}, were estimated by summing the ramet-scale dimensions which were obtained applying ramet allometries for each D_{ramet} (refer to Figure 1 and Table 2).
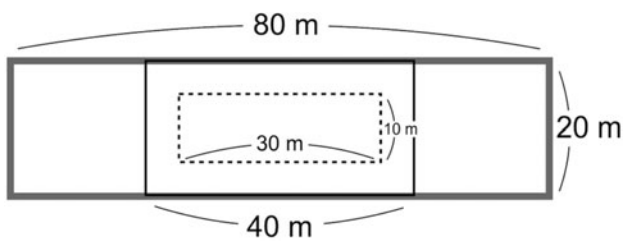
Appendix 3. Scheme of sampling area in permanent plots. The whole 20×80-m plot in grey was used to collect data on crown architecture of trees (D_{tree}, H_{tree} and C_{tree}). The central 20×40-m area in solid black was used to collect data on demography of bamboo ramets and tree biomass dynamics. The central 10×30-m area shown within the dashed line was used to collect data on genet architecture (Appendix 2) and biomass dynamics of bamboos.
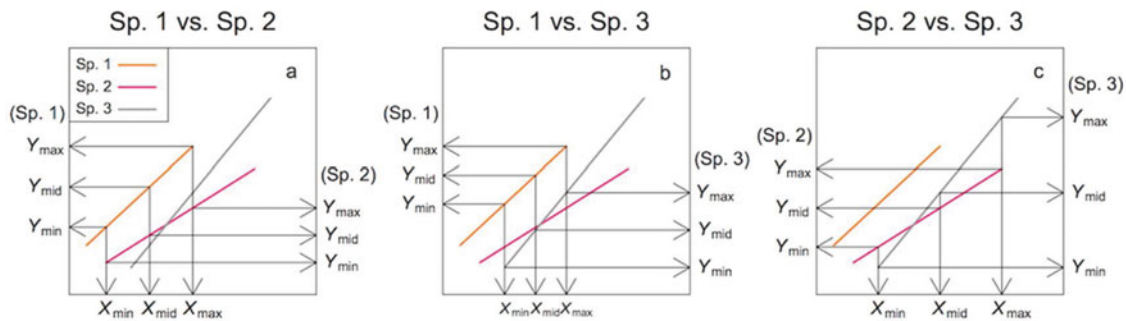
Appendix 4. Allometric comparisons at three reference points on X value. First from an overlapped range between two comparing species, the minimum and the maximum values of the range were determined (X_{min} and X_{max}, respectively), and then, the geometric midpoint, which is the midpoint between $\log(X_{min})$ and $\log(X_{max})$, was determined (X_{mid}). Predicted Y values on reference points were compared between two species: species 1 vs. species 2 (a); species 1 vs. species 3 (b); and species 2 vs. species 3 (c).

Appendix 5. Mean of biomass dynamic rates (y^{-1}). m, wood loss rate; b, wood production rate; r, relative increment rate; N, the number of stems or culms used for the calculation, where the value in parentheses after N represents the number of culms used for b estimation; SD for standard deviation. The value in parentheses after b is estimation including fine-litter production rate, $0.025\ y^{-1}$, obtained by Clark *et al.* (2001) in the Pasoh Forest Reserve in Peninsular Malaysia.

Species	Focal size	N		Average rates (y^{-1})					
				m	SD	b	SD	r	SD
Gigantochloa ligulata	$N_{ramet} \geq 4$	857		0.155	0.0813	0.265	0.177	0.109	0.201
Schizostachyum grande	$N_{ramet} \geq 3$	424	(434)	0.223	0.199	0.426	0.362	0.268	0.435
Trees	$5\ cm \leq D_{tree} \leq 40.4\ cm$	1424		0.0330	0.0741	0.0568 (0.082)	0.0229	0.0238	0.0788

Appendix 6. Variation of LAI and stem basal area (BA) of woody trees among permanent plots before (LAI_{intact}, BA_{intact}) and after (LAI_0, BA_0) timber logging, and change (LAI_{loss}, BA_{loss}) due to logging operation. Column D_{tree} represents lower size limit of trees for calculation. Columns min, average, max, and SD show minimum, average, maximum and standard deviation among 24 permanent plots.

	D_{tree}	Unit	min	average	max	SD
LAI_{intact}	$\geq 45\ cm$	$m^2\ m^{-2}$	0.374	1.70	4.29	1.13
BA_{intact}		$cm^2\ m^{-2}$	2.49	21.1	77.3	19.0
LAI_0	$\geq 45\ cm$	$m^2\ m^{-2}$	0.00	1.42	3.61	0.983
BA_0		$cm^2\ m^{-2}$	0.00	16.1	68.1	15.8
LAI_{loss}	$\geq 5\ cm$	$m^2\ m^{-2}$	0.00	0.788	3.76	1.02
BA_{loss}		$cm^2\ m^{-2}$	0.00	7.11	51.2	12.2