The size at reproduction of canopy tree species in central Africa

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ABSTRACT

Size at reproduction is a key aspect of species life history that is relatively understudied for long-lived tropical trees. Here, we quantified reproductive diameter for 31 major timber species across 11 sites in Cameroon, Congo, and Central African Republic. Specifically, we examined whether (1) between-species variability is correlated with other species traits; (2) reproductive diameter varies within-species among sites; (3) reproductive status varies with crown exposure; and (4) the minimum cutting diameter limits (MCDL) imposed by national forest regulations enable seed trees to persist after logging operations. Consistent with studies conducted elsewhere in the tropics, we found great variability in diameter at reproduction among species, which correlated with adult stature (maximum diameter and height). For some species, reproductive diameter thresholds substantially varied between sites, and crown exposure had a significant positive effect on reproductive status. Most MCDLs were found to be suitable, with trees having a high probability of being seed trees at MCDL. Our findings have implications for the sustainable management of production forests, and they highlight questionable MCDLs for some species and between-site variation in reproductive diameter. The study also highlights the need for long-term phenological monitoring of tree species spanning a large range of ecological strategies to address both theoretical (species life history, allocation trade-offs) and practical questions (MCDL).

Abstract in French is available with online material.

Key words: crown exposure; fruiting diameter; minimum cutting diameter limit; reproductive diameter threshold; reproductive status; sustainable management; timber; tropical wet and moist forests.

RESEARCH ON THE REPRODUCTIVE PHENOLOGY OF TROPICAL FOREST TREES HAS TRADITIONALLY FOCUSED ON TEMPORAL PATTERNS, and revealed a high diversity of reproductive patterns, including sub-annual, annual, supra-annual, and irregular cycles (Newstrom *et al.* 1994, Adamescu *et al.* this volume). By contrast, few quantitative studies have examined the reproductive size of tropical trees (Thomas 2011). Size at reproduction is a key aspect of tree species life history that illustrates the trade-off between resource allocation for growth and reproduction. After germination, trees undergo vegetative growth until they reach a size threshold for reproduction. After this point, trees may exhibit a variety of growth patterns ranging from full cessation of vegetative growth at initiation of reproduction (monocarpic trees such as *Tachigali vasquezii*, Poorter *et al.* 2005) to gradual increases in reproductive allocation across a tree's lifetime (polycarpic trees; Wenk & Falster 2015).

Reproductive size thresholds can be estimated as the inflection point of a logistic regression between tree reproductive status (ability to reproduce or not) and size (Thomas 1996).

Reproductive size thresholds have been quantified for tropical tree species in Malaysia (Thomas 1996, Davies & Ashton 1999), Panama (Wright *et al.* 2005), and Dominica Island (Thomas *et al.* 2015). These thresholds were quantified based on diameter and expressed as a function of height using species-specific allometric equations between height and diameter (Thomas 1996, Wright *et al.* 2005, Thomas *et al.* 2015). Reproductive size thresholds vary greatly among species. For instance, reproductive diameter thresholds varied from 1 to 19 cm among 11 pioneer *Macaranga* species in Malaysia (Davies & Ashton 1999). Also, they were negatively correlated with seed mass and relative shade tolerance: The *Macaranga* species with the highest light requirements had a relatively large reproductive size (maximum height from 6 to 31 m). Light requirement and seed mass were, however, significantly correlated with maximum height, suggesting that these results may have been driven by the positive relationship between maximum height and reproductive diameter. Indeed, species that attained a large stature showed larger reproductive size thresholds than smaller-statured species (Thomas 2011). This pattern is consistent with a systematic cost of reproduction such that early reproduction reduces the resources available for growth after maturity and thus limits maximum tree size (Kozłowski 1992, Obeso 2002).

The proposed trade-off in carbon allocation between growth and reproduction suggests that tree reproductive status is strongly influenced by resource availability, especially light. For instance, in the Democratic Republic of Congo, sun-exposed *Millettia laurentii* trees flowered and fruited regardless of diameter while overtopped trees had a lower probability of flowering and fruiting (Menga *et al.* 2012, minimum sampling diameter of 10 cm). Similarly, in Panama, liana load and crown exposure have significant effects on the relationship between reproductive status and tree size (Wright *et al.* 2005). However, the effect of light availability on reproductive status appears to be species-dependent (Wright *et al.* 2005). For instance, two groups of canopy species were observed in Malaysia (Thomas 1996): one for which reproduction is strongly contingent on crown exposure and the other in which trees begin reproducing at a relatively wide range of sizes while still in the understory.

Besides the importance for species life history, the reproductive size of timber species is critical for selecting seed trees to be left after logging, a key issue for the sustainable management of production forests (Plumptre 1995). In central Africa, trees may only be cut if they are above a minimum cutting diameter. This threshold varies substantially between countries, even for the same species (*e.g.*, Bourland *et al.* 2012). In the few studies addressing the reproductive size of timber species in Africa, reproductive diameters were estimated from the proportion of reproductive trees in 10-cm-wide diameter classes, and an effective reproductive diameter was computed as the minimum or median diameter of the class for which 70 or 80 percent of the trees were reproductive (Doucet 2003, $N = 14$ species in Gabon, Durrieu De Madron & Daumerie 2004, $N = 8$ species in Central African Republic, Menga *et al.* 2012, $N = 1$ species in Democratic Republic of Congo) and from logistic curves fitted to the percentage of reproductive trees against diameter (Plumptre 1995, $N = 16$ species in Uganda). However, the picture is still incomplete for most timber species in central Africa (Fargeot *et al.* 2004).

In this study, we compiled (mostly unpublished) phenology data collected in Cameroon, Congo, and Central African Republic for 31 major timber species in central Africa. We quantified diameter at reproduction, using both the diameter of the smallest reproductive individual and reproductive diameter threshold (Davies & Ashton 1999). First, we explored whether between-species variability can be explained by species traits such as regeneration guild, leaf habit, wood density, adult stature, maximum growth rate, and dispersal mode. We expected that species able to attain a large stature reproduce at a larger size than smaller-statured species (Kozłowski 1992, Obeso 2002, Thomas 2011). Second, we explored within-species variability by testing whether reproductive diameter varied between sites and whether tree reproductive status varied with light availability (crown exposure). We expected little between-site variation in reproductive diameter, as Thomas *et al.* (2015) observed similar reproductive diameters for *Simarouba amara* in Dominica Island and Panama (25.7 and 27.2 cm, respectively). We also expected that light availability only influences reproductive status for some species (Thomas 1996, Wright *et al.* 2005) because of between-species differences in strategy of resource allocation for reproduction (Wenk & Falster 2015). Finally, we assessed the implications of our results for forest management. Specifically, we examined whether the minimum cutting diameter limits (MCDL) currently in force in central African countries can enable seed trees to persist after logging operations.

METHODS

STUDY SITES.—We compiled (mostly unpublished) phenology data collected in 11 sites (Fig. S1) across central African lowland forests (including moist and wet forests, Fayolle *et al.* 2014). Forest technicians monitored phenology in Cameroon between 2004 and 2015 in the logging concessions managed by the companies Pallisco ($N = 3$ sites, Mindourou 1, 2, and 3, Kouadio 2009, Daïnou *et al.* 2012, Bourland *et al.* 2012, Fétéké *et al.* 2015, 2016), Sfid ($N = 2$ sites, Mbang 1 and 2), and Wijma ($N = 2$ sites, Mamfe, Ma'an, Biwolé 2015). In the Congo Republic, they monitored phenology from 2005 to 2011 in the northern part of the country in two logging concessions managed by the company Cib-Olam ($N = 3$ sites, Pokola 1 and 2, and Kabo). In Central African Republic (CAR), they monitored phenology from 1998 to 2003 and from 2005 to 2013 in the M'Baïki experimental site. The sites were located in semi-deciduous forests, except the Mamfe site, which was located in an evergreen forest and the Ma'an site, which was located in a transition zone between the two forest types. Annual rainfall varied from 1550 mm (Mindourou 1–3, Mbang 1–2), 1685 mm (Pokola 1–2, Kabo), 1738 mm (M'Baïki), 2000 mm (Ma'an), to 2477 mm (Mamfe). A pronounced dry season occurs from November to February in Mamfe and M'Baïki (monthly rainfall <100 mm, Worldclim data, Hijmans *et al.* 2005)

and from December to February in Mindourou 1–3, Mbang 1–2, Pokola 1–2, and Kabo. In the latter sites, a reduction in rainfall (short dry season) also occurs in July. The distribution of rainfall is clearly bimodal in the Ma'an site, with two pronounced dry seasons in December–January and in July–August (monthly rainfall <100 mm).

PHENOLOGICAL DATA.—In all sites, experienced forest technicians marked individual trees for monthly phenological monitoring. They measured tree diameter at breast height (dbh) or 30 cm above buttresses prior to monitoring. In all sites except M'Baïki, they also recorded an indicator of crown exposure (a proxy for light availability) following Doucet (2003), and classified trees either as emergent (equivalent to a crown exposure index [CEI] of 5, Clark & Clark 1992), canopy (equivalent to a CEI of 4), or subcanopy (equivalent to CEI of 1–3). In Cameroon and Congo, technicians monitored trees monthly for leaf fall and/or leaf flush, flowering, and fruiting (unripe and ripe fruits were distinguished). For some species, they monitored twice monthly during specific periods to ensure the capture of flowering and/or fruiting events (e.g., *Milicia excelsa* in Mindourou 3, Daïnou *et al.* 2012). Technicians used binoculars to visually evaluate the intensity of each phenological event from the ground on a scale of 0 to 100 percent with an interval of 5 percent, and with an accuracy of 10 percent. They confirmed phenological activity by observing fallen flowers and fruits. In M'Baïki, technicians recorded only the presence of phenological events (and not the intensity) and only the dominant phenophase (either flowering or fruiting). Technicians recorded observations weekly during the 1998–2003 period and twice a month during the 2005–2013 period.

STUDY SPECIES AND POPULATIONS.—From the combined dataset, we identified 57 populations (*i.e.*, a species in a site, Table 1), 31 timber species, 27 genera, and 13 botanical families. Sample size ranged from 10 trees (*Celtis zenkeri*, *Pterocarpus soyauxii*, and *Staudtia kamerunensis*) to 207 trees (*Pericopsis elata*). Minimum and maximum sampled dbh at each site ranged from 10 to 36 cm (median 16 cm) and from 43 to 179 cm (median 105 cm), respectively. The monitoring period ranged from 23 to 94 months, and every population monitored had at least one recorded reproductive event. We assumed that the monitoring period was long enough to capture at least one reproductive event per tree such that trees without observed flowering/fruiting events were considered non-reproductive (43 percent of all monitored trees were non-reproductive). For instance, *Triplochiton scleroxylon*, with supra-annual reproduction (Jones 1974), was monitored for more than 4 yr, and 64 percent of trees of this species were non-reproductive. Nevertheless, we may have erroneously considered some reproductive trees with highly supra-annual cycles to be non-reproductive.

We gathered information on the following species traits from the literature (see Table S1 for values and the complete list of references): regeneration guild (shade-bearer, non-pioneer light-demander, or pioneer), leaf habit (deciduous or evergreen), dispersal mode (wind, animals, or unassisted), maximum height (H_{max}, m), maximum diameter (D_{max}, cm), wood density (Wd, g/cm^3),

and maximum annual growth rate (cm/yr, computed on trees with dbh ≥10 cm at M'Baïki). The study species were mainly deciduous (N = 23 species) and light-demanding (N = 24 pioneer or non-pioneer light-demander species, Table S1), hermaphroditic (N = 26), and either animal-dispersed (N = 15 species) or wind-dispersed (N = 12 species).

ESTIMATING SPECIES REPRODUCTIVE DIAMETERS.—We considered a tree to be reproductive, *that is*, able to produce flowers, if it flowered at least once during monitoring (all fruiting trees were considered flowering trees, although flowers might not have been always observed). For each population (*i.e.*, species × sites), we computed minimum flowering diameter, FlD_{min}, as the smallest diameter observed for a flowering tree. We estimated flowering diameter threshold, FlD_{thr}, from a modified logistic regression model that described tree flowering probability (whether a tree was observed to be flowering during monitoring at least once) as a function of the logarithm of dbh. The following model was fitted using the maximum-likelihood method:

$$P = \exp(a + b * \log(dbh))/[1 + \exp(a + b * \log(dbh))], \qquad (1)$$

where P is the probability of flowering, a and b the intercept and slope of the flowering probability–diameter relationship. We estimated FlD_{thr} as the inflection point of the fitted response curve (Thomas 1996, Fig. 1A–C). This model assumes that the largest trees reproduce at least once during the monitoring period (asymptote = 1). However, for some trees, the monitoring period may have been shorter than their supra-annual cycle (even 8 yr, Bush *et al.* 2017), such that the largest trees reproduce with a probability ≤1 during the monitoring period. To account for this, we fitted a model including an additional constant (asymptote ≤1) but found very similar flowering diameter thresholds (Table S2) and thus report only the results of equation (1). We assessed whether there was a relationship between flowering probability and diameter for the population considered by testing whether the slope b in equation (1) was significantly different from zero. We evaluated the goodness of fit of models using the McFadden determination coefficient (Scott Long 1997) and by the percentage of well-predicted reproductive status as an indicator of prediction accuracy.

To assess potential differences between the ability to flower and the ability to produce seeds, we conducted the same analysis for the probability for bearing ripe fruits. Flowering can be followed by massive flower loss or immature fruit abortion, resulting in no ripe fruits produced (e.g., *P. elata*, Bourland *et al.* 2012). Observers distinguished between ripe and unripe fruits during all phenological monitoring except at the M'Baïki site (CAR) during the first study period (N = 9 populations of 57). We computed the minimum fruiting diameter (FrD_{min}) as the smallest diameter observed for a tree to produce ripe fruits and fruiting diameter threshold (FrD_{thr}) using equation (1).

BETWEEN-SPECIES VARIABILITY IN FLOWERING DIAMETERS.—We examined the relationships between flowering diameter and the

TABLE 1. *List of the 57 populations (i.e., a species in a site), with the number of inventoried months indicated in brackets, sampled size (N), and sampled diameter distribution range (median, minimum, and maximum diameters). For species monitored in several sites, a likelihood ratio test was performed to determine whether the probability to reproduce was site-dependent, and populations were merged when no significant between-site difference was found (P value indicated below species name). For the 48 resulting populations, the number and percentage of flowering and fruiting trees (Nfl (%) and Nfr (%), respectively) and minimum flowering and fruiting diameters (FlD$_{min}$ and FrD$_{min}$, respectively) were computed. For populations with a significant effect of diameter on flowering and fruiting probability (see Table S4), we computed flowering and fruiting diameter thresholds (FlD$_{thr}$ and FrD$_{thr}$, respectively) with 95 percent confidence intervals (in square brackets) from the fitted logistic regressions. Minimum cutting diameter limits (MCDL) are indicated for each population, with the probability for bearing ripe fruits at MCDL (Pfr). The MCDL that were not compared are indicated in brackets.*

Species	Site(s)	Diameter distribution		Flowering variables			Fruiting (ripe fruits) variables			Management variables	
		N	med (range)	Nfl (%)	FlD$_{min}$	FlD$_{thr}$	Nfr (%)	FrD$_{min}$	FrD$_{thr}$	MCDL	Pfr
Afzelia bipindensis	M'Baïki (94)	13	23 (17–69)	5 (38)	28	–	1 (8)	69	–	(80)	
Autranella congolensis	M'Baïki (57)	13	37 (19–104)	3 (23)	37	–				(80)	
Baillonella toxisperma	Mindourou 2 (33),	63	40 (20–140)	15 (24)	65	74 [69;81]	12 (19)	65	85 [77;95]	100	68
$P = 0.427$	Mindourou 3 (33)									100	68
Celtis zenkeri	M'Baïki (57)	10	36 (16–78)	9 (90)	16	–				(70)	
Chrysophyllum boukokoënse	M'Baïki (94)	52	34 (21–66)	47 (90)	21	–	31 (60)	23	30 [28;33]	70	97
Chrysophyllum lacourtianum	M'Baïki (94)	27	33 (22–77)	14 (52)	24	–	2 (7)	60	–	(70)	
Chrysophyllum perpulchrum	M'Baïki (94)	42	36 (21–105)	23 (55)	21	35 [32;39]	16 (38)	21	44 [41;49]	70	91
Detarium macrocarpum	Pokola 1 (71)	15	77 (13–120)	14 (93)	13	–	13 (87)	13	–	(60)	
Entandrophragma angolense	Pokola 1 (70),	62	33 (12–97)	10 (16)	25	66 [57;82]	7 (11)	46	63 [58;72]	80	82
$P = 0.239$	M'Baïki (94)									80	82
Entandrophragma candollei	Pokola 1 (71),	50	39 (12–162)	14 (28)	23	74 [65;87]	10 (20)	52	90 [80;104]	80	39
$P = 0.177$	M'Baïki (94)									80	39
Entandrophragma cylindricum	M'Baïki (94)	88	40 (20–179)	59 (67)	27	36 [34;38]	40 (45)	33	52 [49;56]	80	91
$P < 0.0001$	Mbang 1 (50)	173	62 (11–133)	86 (50)	17	55 [51;60]	59 (34)	22	76 [73;80]	100	77
	Pokola 1 (71)	105	49 (11–138)	19 (18)	44	93 [84;109]	10 (10)	62	106 [96;125]	80	22
Eribroma oblongum	Pokola 1 (71)	73	43 (13–92)	50 (68)	15	28 [25;30]	44 (60)	15	32 [28;35]	60	86
$P = 0.049$	M'Baïki (57)	20	42 (18–89)	11 (55)	18	38 [34;44]				(70)	
Erythrophleum suaveolens	Pokola 1 (71)	65	77 (12–113)	50 (77)	55	55 [50;59]	41 (63)	60	62 [55;67]	60	48
$P < 0.0001$	Mbang 1 (49)	141	60 (18–115)	72 (51)	35	56 [53;59]	1 (1)	61	–	(50)	
	Mbang 2 (69)	43	61 (13–90)	16 (37)	47	69 [62;79]	0 (0)	/	/	(50)	
	M'Baïki (57)	17	55 (26–130)	10 (59)	26	–				(80)	
	Mindourou 3 (87)	39	73 (30–115)	35 (90)	48	–	32 (82)	48	–	(50)	
Khaya anthotheca	M'Baïki (94)	36	26 (20–85)	9 (25)	21	48 [42;56]	5 (14)	51	–	(80)	
Leplaea cedrata	Pokola 1 (71),	44	38 (10–127)	21 (48)	24	38 [34;42]	15 (34)	24	53 [46;61]	60	60
$P = 0.478$	M'Baïki (94)									70	70
Lophira alata	Ma'an (23)	151	40 (10–113)	104 (69)	23	27 [26;28]	97 (64)	23	30 [28;31]	60	99
$P < 0.0001$	Mamfe (24)	198	61 (11–130)	129 (65)	11	36 [32;39]	53 (27)	11	137 [111;191]	60	28
	Pokola 1 (71)	61	55 (10–124)	29 (48)	28	54 [47;61]	13 (21)	33	103 [89;130]	70	27
Lovoa trichilioides	M'Baïki (94)	30	26 (16–110)	3 (10)	44	–	1 (3)	56	–	(80)	
Mansonia altissima	Mindourou 3 (46),	174	41 (10–83)	154 (89)	10	17 [15;18]	90 (52)	18	37 [35;39]	60	80
$P = 0.678$	Mbang 2 (76)									60	80
Milicia excelsa	Mindourou 3 (65)	72	67 (10–160)	55 (76)	37	44 [39;48]	23 (32)	52	105 [89;138]	(100)	
$P < 0.0001$	M'Baïki (94)	31	37 (21–127)	30 (97)	21	–	18 (58)	21	33 [29;37]	(70)	
Millettia laurentii	Pokola 1 (71)	90	48 (11–100)	64 (71)	26	32 [30;35]	49 (54)	26	42 [39;45]	60	79
Nauclea diderrichii	Pokola 1 (71)	21	75 (11–109)	17 (81)	56	–	17 (81)	56	–	(60)	
Pericopsis elata	Mindourou 1 (61),	327	65 (15–105)	292 (89)	15	30 [28;32]	83 (25)	36	108 [97;128]	90	41
$P = 0.061$	Mbang 1 (63)									90	41
Petersianthus macrocarpus	M'Baïki (57)	19	64 (21–140)	16 (84)	33	–				(70)	

(continued)

Table 1 (continued)

Species	Site(s)	Diameter distribution		Flowering variables			Fruiting (ripe fruits) variables			Management variables	
		N	med (range)	Nfl (%)	FlD_{min}	FlD_{thr}	Nfr (%)	FrD_{min}	FrD_{thr}	MCDL	Pfr
Pouteria altissima	M'Baïki (94)	52	39 (22–100)	26 (50)	26	39 [36;42]	16 (31)	27	51 [47;56]	70	82
Pterocarpus soyauxii	Mbang 1 (47),	85*	39 (12–100)	26 (31)	38	51 [47;55]	6 (7)	41	–	(60)	
$P = 0.090$	Mbang 2 (69),									(60)	
	Pokola 1 (71),									(80)	
	M'Baïki (57)									(60)	
Pycnanthus angolensis	M'Baïki (57)	18	51 (25–97)	16 (89)	30	–				(80)	
Ricinodendron heudelotii	M'Baïki (57)	18	70 (36–138)	16 (89)	43	–				(70)	
Staudtia kamerunensis	Pokola 1 (71)	10	79 (10–112)	10 (100)	10	–	10 (100)	10	–	(40)	
$P = 0.008$	M'Baïki (57)	19	43 (23–66)	11 (58)	23	–				(50)	
Sterculia rhinopetala	Mbang 2 (76)	131	43 (11–86)	76 (58)	12	35 [33;37]	65 (50)	22	41 [40;43]	50	79
Terminalia superba	Pokola 1 (71)	28	45 (11–75)	21 (75)	30	30 [26;33]	19 (68)	30	34 [29;38]	60	95
$P < 0.0001$	Mindourou 3 (60)	39	59 (23–116)	38 (97)	23	–	28 (72)	32	–	(60)	
	Mbang 1 (46)	83	49 (24–81)	4 (5)	33	–	0 (0)	/	/	(60)	
Triplochiton scleroxylon	Mindourou 3 (47)	80	61 (19–99)	37 (46)	39	61 [57;66]	0 (0)	/	/	(80)	
$P = 0.003$	M'Baïki (94)	97	73 (25–148)	50 (52)	45	67 [61;72]	29 (30)	56	106 [94;125]	60	21
	Pokola 2 (71)	29	62 (28–120)	12 (41)	28	71 [64;79]	1 (3)	71	–	(70)	
	Mbang 2 (75)	180	55 (11–133)	44 (24)	38	95 [86;109]	0 (0)	/	/	(80)	
	Kabo (71)	47	62 (17–149)	13 (28)	46	95 [82;120]	4 (9)	71	–	(70)	

*The total number of *P. soyauxii* trees not including the M'Baïki site was $N = 68$.

seven traits gathered from the literature. We used Kruskal–Wallis rank sum tests to test for significant differences in flowering diameter (FlD_{min} or FlD_{thr}) between the levels of qualitative traits (regeneration guild, leaf habit, and dispersal mode). We used asymptotic Spearman correlation tests (adapted to handle equally ranked species via permutation tests) to evaluate relationships between FlD_{min} and FlD_{thr} and species quantitative traits (Wd, D_{max}, H_{max}, and maximum growth rate). For species with populations in several sites, we used FlD_{min} and FlD_{thr} estimated over all populations.

BETWEEN-SITE DIFFERENCES AND EFFECT OF LIGHT AVAILABILITY ON FLOWERING PROBABILITY.—We tested for between-site differences in flowering probability (regardless of diameter) for the 15 species shared among at least two sites. We fitted the following logistic regression model:

$$P = \exp(a + b * \log(\text{dbh}) + c * \text{Site}) / [1 + \exp(a + b * \log(\text{dbh}) + c * \text{Site})], \quad (2)$$

where P, a, and b are the same as in equation (1), and c quantifies the effect of the site on P. We used a likelihood ratio test between equations (1) and (2) to determine whether P was significantly site-dependent.

To explore the effect of light availability on tree flowering probability, we tested whether trees within different crown exposure categories ('subcanopy', 'canopy', or 'emergent') in a population had different flowering probabilities (regardless of diameter)

using the same approach as for the effect of site. We thus fitted the following logistic regression model:

$$P = \exp(a + b * \log(\text{dbh}) + d * \text{CE}) / [1 + \exp(a + b * \log(\text{dbh}) + d * \text{CE})], \quad (3)$$

where P, a, and b are the same as in equation (1), and d quantifies the effect of tree crown exposure on P. We used a likelihood ratio test to contrast equations (1) and (3) to determine whether crown exposure has a significant effect on P. To test for the effect of tree crown exposure on flowering probability, we used data from the 15 populations with at least 10 trees in each of the three categories of crown exposure, corresponding to nine species in seven sites in Cameroon and Congo.

MCDL SUITABILITY.—To assess the suitability of minimum cutting diameter limits (MCDL) that are species- and country-specific (Table S3), we used the logistic regressions to compute the probability of being a seed tree (*i.e.*, bearing ripe fruits) at MCDL (Fig. 1D). For dioecious species (*M. excelsa*, *S. kamerunensis*, *Ricinodendron heudelotii*, and *Pycnanthus angolensis*, Table S1) the analysis was not conducted because the probability of a tree being a seed tree at MCDL also depends on the probability of a tree being female.

We conducted all analyses using R software (R Core Team 2016), including logistic regressions fitted with the glm() function, asymptotic Spearman correlation tests with the package 'coin' (Zeileis *et al.* 2008), and McFadden's pseudo R^2 with the package 'pscl' (Jackman 2015).
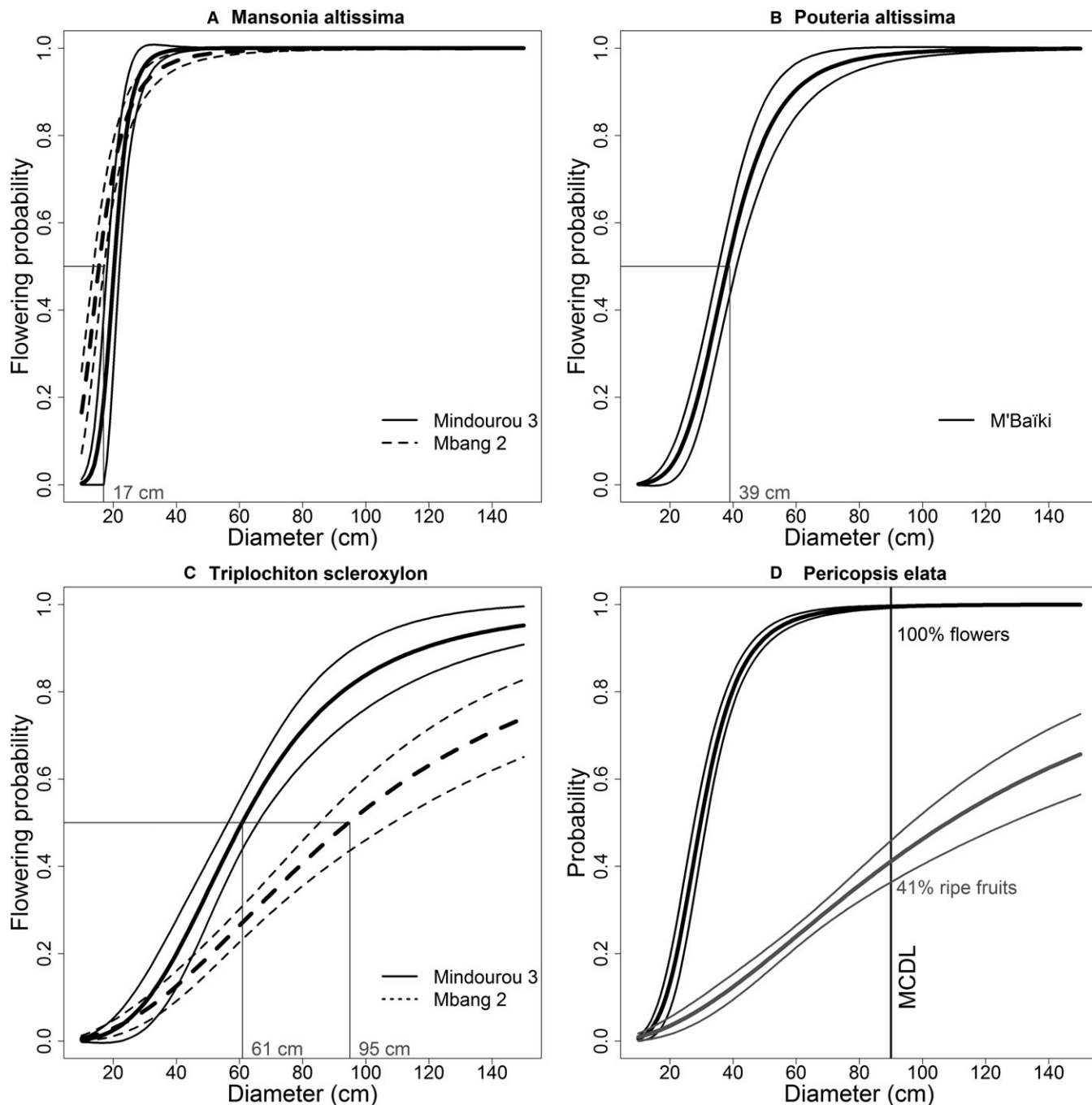
FIGURE 1. Logistic regressions between tree flowering probability and diameter for species with low (FlD$_{thr}$ = 17 cm, A), medium (39 cm, B), and high (from 61 to 95 cm, C) flowering diameter thresholds. Species *Mansonia altissima* in (A) did not show significant between-site differences in reproductive size, contrary to *Triplochiton scleroxylon* in (C). In (D), the methodology for estimating the suitability of MCDL (here 90 cm, vertical line) by computing tree probability for bearing ripe fruits at MCDL is illustrated.

RESULTS

BETWEEN-SPECIES VARIATION IN FLOWERING DIAMETER.—The size at reproduction varied among the 31 timber species studied: Minimum flowering diameter (FlD$_{min}$) ranged from 10 cm (*Mansonia altissima*) to 65 cm (*Baillonella toxisperma*, Fig. 2). One-third of the study species (N = 11 of 31 species) flowered at relatively small size (FlD$_{min}$ between 10 and 28 cm), corresponding to the minimum diameter sampled (Table 1). It is thus possible that these species may be able to flower at even smaller diameters.

We found a significant relationship between tree flowering probability and dbh for 19 of the 31 species tested. Although

significant the strength of the relationship showed notable variability with McFadden's pseudo R^2 ranging from 15 to 70 percent (and the accuracy of predictions ranged from 67 to 96 percent, Table S4). Among the 19 species, flowering diameter thresholds (FlD$_{thr}$) ranged from 17 cm (*M. altissima*) to 76 cm (*T. scleroxylon*, Fig. 2). As expected, flowering diameter thresholds increased with species adult stature, reflected in the significant positive correlation between FlD$_{thr}$ and D$_{max}$ (Spearman's *rho* = 0.70, *P* = 0.003) and between FlD$_{thr}$ and H$_{max}$ (*rho* = 0.59, *P* = 0.012, Fig. 3). FlD$_{min}$ was also significantly positively correlated with species maximum growth rate (*rho* = 0.55, *P* = 0.006, Fig. 3): Fast growing species tended to have larger minimum flowering diameters than slower-growing species. We did not find any significant correlation between flowering diameters and any other traits examined (wood density, regeneration guild, leaf habit, and dispersal mode).

WITHIN-SPECIES VARIATION IN FLOWERING DIAMETER.—We identified significant between-site differences in flowering probability for eight of the 15 species tested (Table 1). Flowering diameter thresholds (FlD$_{thr}$) differed greatly between sites for these species

(Table 1, Fig. 1C). *Entandrophragma cylindricum* had a FlD$_{thr}$ 2.6-times larger in Congo (93 cm at Pokola 1) than in the CAR (36 cm at M'Baïki), with an intermediate value in Cameroon (55 cm at Mbang 1). Large between-site differences in FlD$_{thr}$ were also observed for *T. scleroxylon* (from 61 to 95 cm) and *Lophira alata* (from 27 to 54 cm). Moreover, the strength of the relationship between tree flowering probability and diameter can also substantially vary among sites. For instance, McFadden's pseudo R^2 varied from 15 (Mbang 2) to 61 percent (Pokola 1) for *Erythrophleum suaveolens* and from 18 (Mamfe) to 64 percent (Ma'an) for *L. alata* (Table S4). This suggests that tree flowering probability may be influenced by factors other than diameter at Mbang 2 and Mamfe for *E. suaveolens* and *L. alata*, respectively.

As expected, the effect of crown exposure was species-specific. Crown exposure was significantly related to tree flowering probability for six of the 15 populations tested, corresponding to six of nine species (Table 2). Regardless of diameter, subcanopy trees had a lower flowering probability than canopy and emergent trees for *Eribroma oblongum* in Pokola 1, *L. alata* in Mamfe, and *P. elata* in Mindourou 1. Emergent trees had a higher flowering probability than subcanopy and canopy trees for *E. cylindricum*
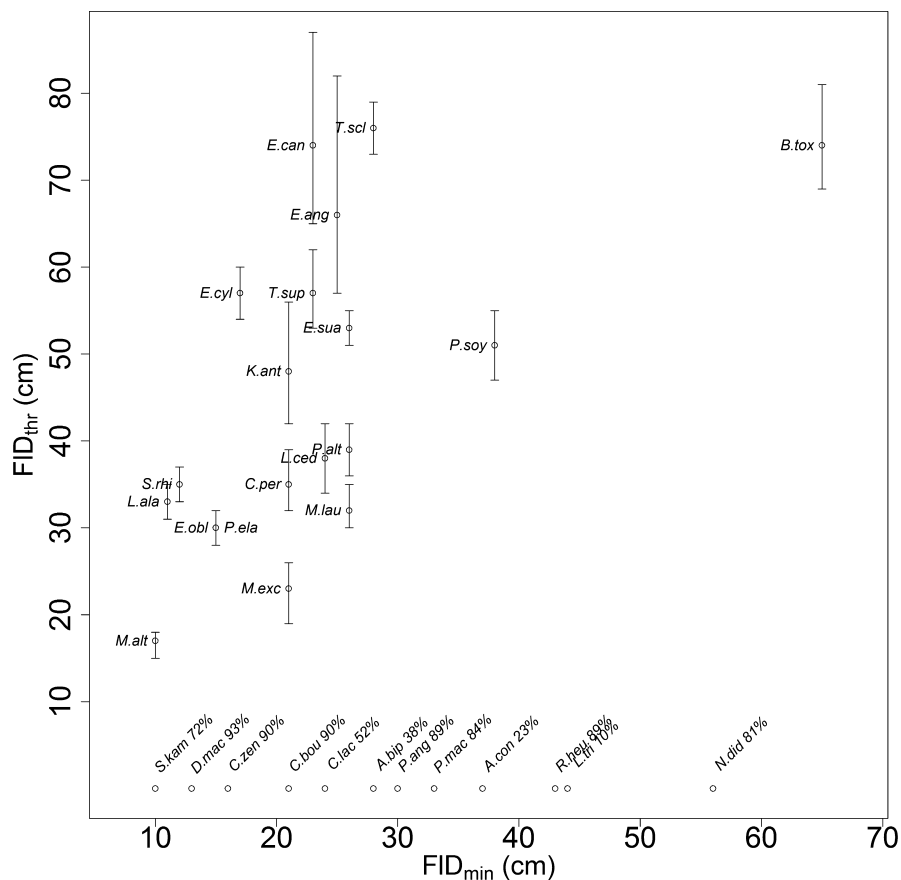

FIGURE 2. Flowering diameter threshold (FlD$_{thr}$), with 95 percent confidence intervals as a function of minimum flowering diameter (FlD$_{min}$) for the 19 species with a significant relationship between flowering probability and diameter (Spearman's *rho* = 0.64, *P* = 0.007). For the 12 other species, FlD$_{min}$ only is indicated at the bottom, with the percentage of flowering trees. Note that species could display significant variation in flowering diameter with site (see Table 1).

and *E. suaveolens* in Mbang 1 and for *T. scleroxylon* in Mbang 2. Nevertheless, this significant effect was observed only at these specific sites (except for *E. oblongum*, Table 2). This suggests that the effect of crown exposure on tree flowering probability varies according to forest characteristics, such as forest structure and light availability under the canopy.

FRUITING DIAMETERS AND MINIMUM CUTTING DIAMETER LIMITS.— When assessing the probability of a tree bearing ripe fruits, we found that the minimum fruiting diameter was higher than the minimum flowering diameter (≥10 cm) for 10 of the 26 species examined (Table 1, Fig. 4A). Fruiting diameter thresholds were significantly higher than the flowering diameter thresholds for all but four species (Table 1, Fig. 4B).

To evaluate the suitability of minimum cutting diameter limits (MCDL), we computed the probability of a tree bearing ripe fruits at MCDL. This was possible for 17 hermaphrodite species and 27 populations (Table 1). Eleven species had at least 60 percent probability of being seed trees at MCDL, which is an acceptable level. By contrast, *Entandrophragma candollei*, *E. suaveolens*, *P. elata*, and *T. scleroxylon* had between 21 and 48 percent

probability of being seed trees at MCDL, despite some species having a high probability of being able to flower at MCDL (Fig. 1D). Evaluations of the MCDL for *E. cylindricum* and *L. alata* varied by site due to significant intersite variation in fruiting diameter (Table 1). The MCDL of *E. cylindricum* was apparently insufficient in Congo but was likely suitable in Cameroon and CAR, with trees having 22, 77, and 91 percent probability of being seed trees at MCDL, respectively. Similarly, the MCDL of *L. alata* was insufficient in Congo and in the Ma'an site in Cameroon but apparently suitable in the Mamfe site in Cameroon, with trees having 27, 28, and 99 percent probability of being seed trees at MCDL, respectively.

DISCUSSION

THE REPRODUCTIVE SIZE OF MAJOR TIMBER SPECIES IN CENTRAL AFRICA.—The 31 timber species studied include most of the logged species in central Africa (Bayol *et al.* 2012). These trees are large-sized, widespread, and/or locally abundant and thus significantly contribute to forest regional aboveground biomass stocks (Bastin *et al.* 2015). We found highly variable reproductive
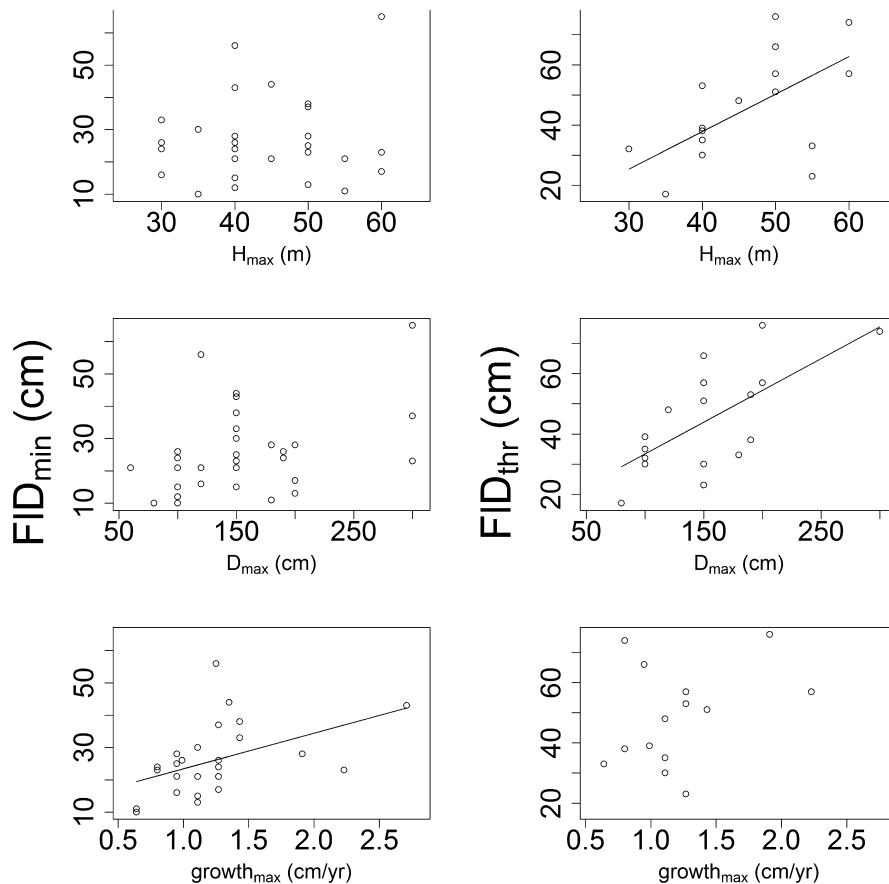

FIGURE 3. Correlations between flowering diameter variables (minimum flowering diameter, FlD_{min}, and flowering diameter threshold, FlD_{thr}) and species maximum height (H_{max}), maximum diameter (D_{max}), and maximum growth rate ($growth_{max}$). Data were analyzed by Spearman's correlation test, and significant correlations are indicated with a black line ($P < 0.05$).

TABLE 2. *Distribution of sampled trees in the three categories of crown exposure (subcanopy, canopy, and emergent), with the percentage of reproductive trees within each category indicated in parenthesis. We tested for a significant effect of crown exposure on flowering probability using a likelihood ratio test for which a p-value is indicated (P < 0.05 is indicated in bold). Categories with a significantly different percentage of flowering trees are indicated with an asterisk.*

Species	Site	Subcanopy	Canopy	Emergent	P
Baillonella	Mindourou 2	32 (0)	5 (40)	4 (25)	–
toxisperma	Mindourou 3	4 (0)	5 (100)	13 (54)	–
Detarium	Pokola 1	2 (100)	7 (86)	6 (100)	–
macrocarpum					
Entandrophragma	Pokola 1	10 (0)	3 (33)	1 (0)	–
angolense					
Entandrophragma	Pokola 1	13 (15)	6 (33)	12 (67)	–
candollei					
Entandrophragma	Mbang 1	70 (27)	47 (53)	**51 (82)***	**0.045**
cylindricum	Pokola 1	44 (9)	38 (24)	23 (26)	0.475
Eribroma oblongum	Pokola 1	41 **(46)***	20 (95)	12 (100)	**0.024**
Erythrophleum	Mbang 1	84 (36)	34 (65)	23 **(87)***	**0.044**
suaveolens	Pokola 1	20 (35)	22 (91)	23 (100)	0.083
	Mindourou 3	6 (83)	15 (100)	18 (83)	–
	Mbang 2	34 (35)	6 (33)	3 (67)	–
Leplaea cedrata	Pokola 1	13 (31)	14 (71)	5 (100)	–
Lophira alata	Mamfe	68 **(37)***	39 (67)	89 (88)	**0.006**
	Pokola 1	23 (30)	13 (38)	25 (68)	0.965
	Ma'an	75 (49)	49 (98)	27 (70)	0.825
Mansonia altissima	Mbang 2	93 (84)	13 (92)	14 (100)	0.239
	Mindourou 3	17 (88)	28 (93)	9 (100)	–
Milicia excelsa	Mindourou 3	7 (14)	40 (88)	21 (90)	–
Millettia laurentii	Pokola 1	48 (58)	35 (86)	7 (86)	–
Nauclea diderrichii	Pokola 1	3 (0)	8 (88)	10 (100)	–
Pericopsis elata	Mindourou 1	48 **(62)***	81 (99)	78 (97)	**0.016**
	Mbang 1	53 (79)	41 (100)	22 (95)	0.205
Pterocarpus	Pokola 1	6 (0)	3 (33)	1 (0)	–
soyauxii	Mbang 1	8 (38)	3 (67)	9 (44)	–
	Mbang 2	21 (5)	5 (20)	12 (42)	–
Staudtia	Pokola 1	3 (100)	2 (100)	5 (100)	–
kamerunensis					
Sterculia	Mbang 2	81 (42)	19 (79)	30 (90)	0.638
rhinopetala					
Terminalia	Mbang 1	34 (3)	29 (10)	16 (0)	0.205
superba	Pokola 1	9 (56)	10 (80)	9 (89)	–
Triplochiton	Mbang 2	105 (10)	27 (37)	47 **(49)***	**0.046**
scleroxylon	Kabo	18 (11)	16 (44)	13 (31)	0.388
	Pokola 2	14 (14)	6 (67)	9 (67)	–
	Mindourou 3	9 (11)	51 (47)	20 (60)	–

diameter thresholds among species, in accordance with previous studies on tropical tree species from Malaysia (Thomas 1996, Davies & Ashton 1999), Panama (Wright *et al.* 2005), and Dominica Island (Thomas *et al.* 2015). The minimum flowering diameter ranged from 10 cm (*M. altissima*) to 65 cm (*B. toxisperma*); however, 10 cm was the minimum sampled diameter, suggesting that the actual minimum could be lower. Among the 19 species showing a significant relationship between reproductive status and diameter, the flowering diameter thresholds ranged from 17 cm (*M. altissima*) to 76 cm (*T. scleroxylon*). For the 12 remaining species, the absence of a significant relationship likely resulted from inadequate sampling (Fig. S2). Less than 20 trees were sampled for eight of these 12 species, and for the four other species, almost all trees in the population were either reproductive or immature. We therefore recommend that future studies should sample a minimum of 20 trees and adopt species-specific minimum sampling diameters (*e.g.*, Wright *et al.* 2005) to ensure sampling of both reproductive and immature trees.

The positive relationship observed between flowering diameter threshold and adult stature is consistent with previous studies conducted elsewhere in the tropics (Thomas 1996, Davies & Ashton 1999, Wright *et al.* 2005, Thomas *et al.* 2015). This is further evidence of a general trade-off of resource allocation between growth and reproduction (Kozłowski 1992, Obeso 2002), such that early allocation to reproduction limits the growth after maturity, reducing the ability to attain large size. We also found a positive correlation between minimum flowering diameter and maximum growth rate: Species able to achieve fast growth tended to have higher minimum flowering diameter than slower-growing species. This suggests that species that invest heavily in growth (high growth potential) have reduced ability to reproduce early (first reproduction at larger diameter). This pattern should be further explored using a larger set of species with differing ecological niches, in contrast to the mainly long-lived, light-demanding species observed in this study.

In a study of 53 Dominican, Panamanian, and Malaysian tree species spanning a broad range of ecological strategies, Thomas *et al.* (2015) also found evidence for a trade-off between growth and reproduction, with a negative correlation between species wood density and relative height at maturity. Assuming that low wood density is associated with high potential growth rate, this finding suggests that faster-growing early-successional trees tend to have a reproductive height closer to their maximum height than slow-growing late-successional species. These results seem in contradiction with the common hypothesis that pioneer species reproduce early (*e.g.*, *Musanga cecropioides*, Swaine & Whitmore 1988, Turner 2001), but what actually was hypothesized is an early reproduction on a temporal scale, and fast growing tree species may still reproduce at a younger age, but at a greater size, than slow-growing tree species.

The finding that diameter thresholds for fruit production exceeded those of flower production for 13 of the 17 examined species is also evidence of a growth-reproduction allocation trade-off. In polycarpic trees, reproductive allocation gradually increases with age (Wenk & Falster 2015). Assuming the metabolic costs of fruit production are higher than flower production, it is reasonable for fruits to be produced at higher diameter thresholds than flowers when resources are sufficient. Similarly, flowers with only the male function that is functional
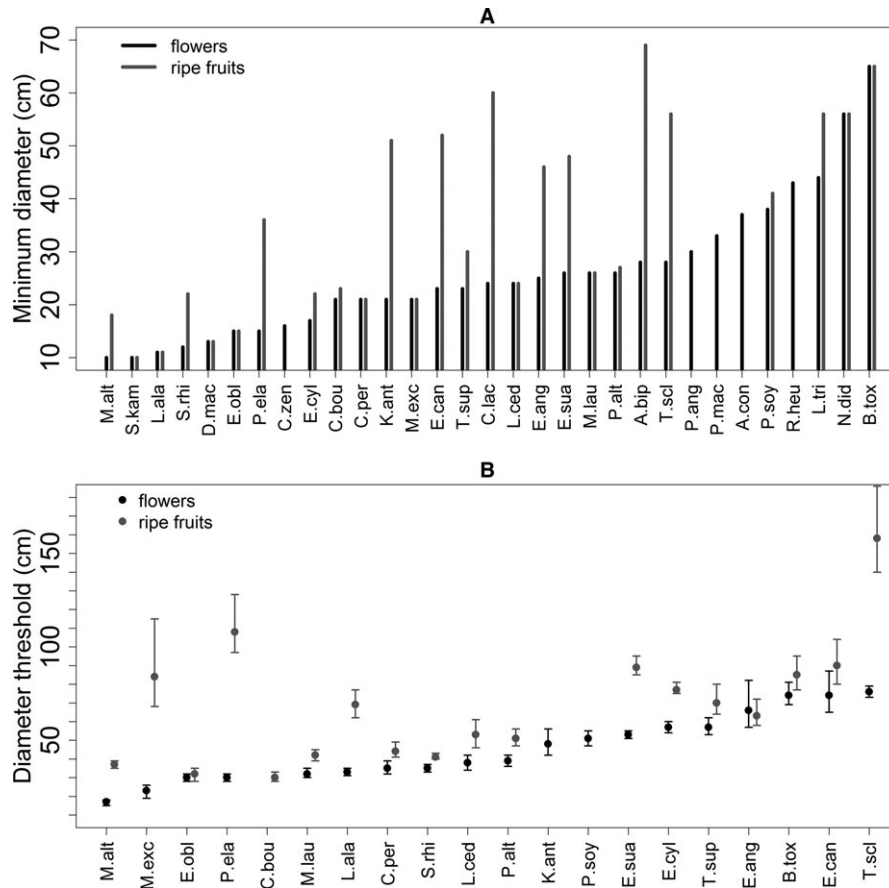
FIGURE 4. Comparison of flowering and fruiting diameters. (A) Minimum flowering and fruiting diameters for the 31 species (black and gray bars, respectively). (B) Flowering and fruiting diameter thresholds (black and gray points, respectively), with their 95 percent confidence intervals. In (B), flowering diameter thresholds were estimated for 19 species and fruiting diameter thresholds for 18 species.

(unable to produce mature fruits) are produced at a smaller tree size than flowers with both functional male and female structures. A smaller size of initial reproduction has been observed for male versus female trees of dioecious tropical species (*e.g.*, Thomas & LaFrankie 1993, Queenborough *et al.* 2007), likely due to the greater per gamete cost of reproduction for females than males. An analogous pattern was also found in a tropical rain forest palm showing labile sex expression: The species initially reproduces as a male in the understory, and as it grows and enters the energy-rich canopy, the cost restraints on fruit production are relaxed, and female function can be realized (Voeks 1988).

For some species, flowering size thresholds can show substantial within-species variation between sites (*e.g., E. cylindricum, T. scleroxylon*). Also, the importance of size in predicting flowering probability can strongly vary within species between sites (*e.g., E. suaveolens, L. alata*). Although sample size, diameter distribution, and length of the monitoring period were not strictly comparable between sites, we believe that this between-site variation in flowering diameter thresholds results from between-site variation in resource availability. We found that crown exposure to light significantly influenced tree reproductive status only for some

species, as previously reported (Thomas 1996, Wright *et al.* 2005), but also only at specific sites. This suggests that the effect of crown exposure may depend on the overall light availability in the site. For instance, the effect of crown exposure found for *L. alata* in Mamfe but not in Ma'an could be explained by a difference in forest maturity associated with a difference in forest structure. In Mamfe, an old growth forest, there are more tall and large trees (leading to a stronger light gradient) than in Ma'an, a younger secondary forest (A. Biwolé, *pers. comm.*). Therefore, the lower flowering probability found for subcanopy trees in Mamfe could result from the trees receiving lower light levels than the subcanopy trees in Ma'an. However, other factors may be involved, as climatic conditions and soil types strongly differ between these two sites.

THE SUITABILITY OF MCDL.—We found the MCDL suitable for most of the species studied. MCDLs were likely insufficient for *E. suaveolens* at two specific sites in Cameroon (Mbang 1 and 2) and for *T. scleroxylon* at all sites, for which none or very few fruiting trees were found during the monitoring period of at least 4 yr. Very low fruiting levels for *T. scleroxylon* have been observed previously (Jones 1974) and were attributed to its massive natural

loss of flowers (Ashiru 1975) and parasitism of unripe fruits (Mallet 1986). The fact that some trees may only appear to be reproductive underlines the complexity of managing timber resources via natural regeneration. Also, if seed production is an increasing function of diameter, the impact of logging may still be quite large, pointing to the need to better quantify this relationship. Furthermore, the presence of seed trees in the stand does not necessarily ensure effective regeneration (Swaine & Hall 1988). Most central African timber species are light-demanding and cannot regenerate under the low logging intensities typically applied (Karsenty & Gourlet-Fleury 2006). The lack of regeneration of these species, which now dominate the canopy, likely began around 1850, after major anthropogenic disturbances ceased (Morin-Rivat et al. 2017). As common logging operations do not create openings large enough to guarantee the natural regeneration of these species (e.g., P. elata included on CITES Appendix II and recorded as endangered in the IUCN Red List, Bourland et al. 2015), complementary treatments such as enrichment planting in logging gaps (e.g., Doucet et al. 2009) or plantations in degraded forest areas (Doucet et al. 2016) are needed to ensure the sustainable management of these species.

ACKNOWLEDGMENTS

DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8t026 (Ouédraogo et al. 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Location of the 11 study sites across central Africa with the number of species and trees monitored, and monitoring period.

FIGURE S2. Diameter distribution of all sampled trees and of flowering ones for the populations for which FlD$_{thr}$ could not be estimated.

TABLE S1. *List of the 31 timber species with their scientific name and botanical family.*

TABLE S2. *List of the 57 populations with parameters of the model described in equation (1) and parameters of a model with an asymptote ≤1.*

TABLE S3. *List of the 31 timber species with their commercial name in Cameroon, scientific name, and minimum cutting diameter limits in Cameroon, Congo Republic, and Central African Republic.*

TABLE S4. *List of the 57 populations with the parameters of the logistic regressions between tree diameter and probability for bearing flowers and ripe fruits.*

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