Mast fruiting in a large tropical African legume tree provides evidence for the nutrient resource limitation hypothesis

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Abstract

The large grove-forming tropical tree *Microberlinia bisulcata* (Fabaceae subfamily Detarioideae) at Korup, Cameroon, shows strong mast fruiting. Reproductive allocation is considerable. The site has very nutrient-poor soil. To test the nutrient resource limitation hypothesis, phenological recordings between 1989 and 2017 were matched with climate variables, and analyzed using logistic time-series regression. Masting happened mostly on 2- or 3-year cycles. A strong predictor was mean daily rainfall in the dry season: low in the current year of masting and high in the year prior. Less strongly predictive was the increase in dry season radiation between prior and mast years. Masting events showed no relationship to annual stem increment, nor with local plantation yields. Later, the normally heavy mastings became moderate after two attacks by caterpillars. Collated studies of fallen leaf nutrient concentrations showed that P increased markedly, K rose and fell, but N and Mg changed little, in the inter-mast interval. P and K were likely being accumulated and stored, and then triggered masting events when internal thresholds were crossed. The drier season prior to masting enabled a rise in C, and the wetter season the year before, with higher soil moisture, enabled better acquisition and uptake of nutrients by roots and mycorrhizas. The main storage of P may be in bark and branches, that for K on soil organic-colloids. A rooting-fruiting trade-off in C allocated over a minimal 2-year cycle is implied. Hypothesized is that synchrony among masting trees may be achieved, in part, by an equilibration of P across the mycorrhizal network. The long-term driver appears to be the inherent year-to-year stochasticity of dry-season rainfall, realization of which leads to an important refinement of the hypothesis. Life history strategy linked to nutrient resource dynamics provides a plausible explanation and more advanced hypothesis for the masting events observed.

Keywords Detarioideae, dry season intensity, ectomycorrhizas, Fabaceae, lowland rain forest, mast fruiting, nutrient limitation, phosphorus and potassium, soil moisture, times-series analysis, western Central Africa.

Introduction

By fruiting and seeding intensively at intervals as opposed to continuously over the years, seed and seedling survival may be enhanced for plants species with a masting iteroparous type of life-history as an evolutionary stable strategy [1-3]. Trees provide by far the majority of the documented cases. To explain how a species' fitness can be maintained or increased, a so-called 'economy of scale' concept has often been invoked. Three general processes have been proposed to achieve this type of economy, usually thought of, teleonomically, as the ultimate causes of mast fruiting and seeding: (1) the efficacy of pollination may be increased by mass flowering, (2) seed predators may be more readily satiated by mass seeding, and (3) the chances of successful dispersal and establishment may be improved by larger reproductive output [4-7]. Much of the reported research into masting, however, has been in the ecological and evolutionary direction with a strong temperate-biome bias (see reviews aforementioned). Surprisingly, there have been comparatively very few studies on masting in the tropics (e.g. [8-11]).

A much more critical issue for understanding masting in trees is the present lack of evidence for, and hypotheses about, the physiological mechanisms which *enable* mast fruiting and seeding, for both temperate and tropical ecosystems. These mechanisms are commonly viewed by ecologists as being proximate causes. Recent discussions about whether a strict distinction between ultimate and proximate causes exists [12, 13] leave it

more open that factors, such as nutrient supply, directly affecting physiological processes might also qualify as ultimate causes of mast fruiting [14, 15], although it has been contested whether they can constitute an 'economy of scale' [16].

For flower, fruit and seed production to be allocated efficiently over the life-time of the adult tree as masting years, a set of physiological resource-mechanisms, probably in serial form, must be in place [17]. Resource budget models, initiated by Isagi et al. [18], have simulated how a resource, usually carbon (C), accumulates in storage to an internal plant threshold which then triggers flowering. Almost all such models have involved the coupled wind pollination of neighbouring individuals [19-24]. They have often involved the Moran effect whereby masting is synchronized over large distances by driving climate factors. The triggering is thought to be brought about by a resource level being crossed in the plant which affects plant hormone concentrations that then cue a leafing axil to change to a flowering one, and finally enable fruit maturation (see e.g. [25]). In this respect, an individual tree can be modeled as an integrated and dynamic system which controls the timing and intensity of reproductive allocation to masting. Details of the physiological mechanisms can be expected to differ across tree species and sites, each achieving a stable yet flexible masting strategy in a different way.

The evidence for C as the main resource directly involved in masting is, however, quite weak. This conclusion comes from direct measurements on whole trees and observations of allocation and experimental manipulation of branches; and from overall C budgets and studies on the dynamics of non-structural carbohydrates (NSCs) [26-37]. A few studies have suggested that mineral nutrients may be the key resources underlying budget mechanisms, but the evidence remains scarce because the topic has been so little researched. So far, Han et al. [38] and Han and Kabeya [39], have shown that nitrogen (N) storage and mobilization is important for triggering flowering in *Fagus*. Fernandez-Martinez et al. [40]

and Le Roncé et al. [41] have indicated that phosphorus (P) and zinc (Zn), and N and Zn, respectively are likely involved in mast fruiting of temperate trees more widely. Carbon should not be laid aside completely as a co-resource though. It is needed with N, phosphorus (P), potassium (K), and other macronutrients, not just to build fruits and seeds, but also indirectly to support growth and maintenance of organs such as fine roots and mycorrhizas which are essential for nutrient acquisition.

If macronutrients do lie behind the mechanisms of mast fruiting it could be expected that the element most important in controlling reproduction might be the one which is at the lowest level of availability at the site relative to the others, the one that is in most critical supply overall for the trees [14, 42]. This element will need to be accumulated in order to support successful reproduction, because seed filling depends on minimally attaining the necessary stoichiometric ratios for all elements required, and doing so without undue costs to other tree growth and maintenance demands in the short to medium term. Further, 'extra-stoichiometric' requirements may need to be met where the same element's availability is very low in the soil: a rise in seed concentration would be advantageous for seedling establishment.

In this way natural selection would be expected to evolve a cueing-threshold-triggering system using the critical nutrient in the form of a cell storage product. Other elements being in not quite so low supply as the first will also be important, which leads to the idea of nested systems of stores and thresholds. The search, then, is for those key limiting elements that most determine tree growth rates and nutrient cycling, which can also be shown to determine frequency and intensity of reproduction. Whilst the particular elements involved are probably different for different species, habitats and ecosystems, in principle, the same fundamental process overall can be postulated to operate.

114 Artificial selection of trees for fruiting under controlled nursery conditions has
115 provided a major insight into tree physiology with regard to fruiting and what may lie as the
116 basis to masting [43-46]. Cultivated trees often follow an 'alternating bearing' fruiting
117 schedule, with years of 'on' and 'off' harvests over a regular 2-year period. Several temperate
118 tree species in the Fagaceae show such an alternating pattern in natural forest, which leads to
119 the idea that, theoretically, the minimal-intrinsic model across all masting species is perhaps
120 alternating years of reproduction [10], but in artificially non-fertilized situations the interval
121 between fruitings becomes extended beyond 1 year to allow time to accumulate critical
122 resources and thus allow masting to effect maximize fitness. ('Interval' is defined by the
123 years of non-masting between masting events.) How the tree system is coordinated, in order
124 to synchronize mast fruiting, is a central issue? Nutrient cycles have been strongly implicated
125 in several fruit tree studies (e.g. [47, 48], and see later Discussion).

126 The main hypothesis of the present paper is that limiting mineral nutrients can
127 determine mast fruiting at the mechanistic, tree-physiological and proximate/ultimate level,
128 particularly for those species that are ectomycorrhizal. This limitation is expected to be
129 strongest where soil mineral nutrients at a site are in critically low supply and
130 ectomycorrhizas are essential to nutrient uptake. Both the tropical Fabaceae subfamily
131 Detarioideae and the Dipterocarpaceae are often ectomycorrhizal [49-51] and both commonly
132 do show mast fruiting. Among the temperate families (Fagaceae and Pinaceae especially)
133 there is a strong association too between masting and having this symbiotic mode of nutrient
134 uptake [52]. Recently though, apart from the review of Corrales et al. [53], the potential role
135 of ectomycorrhizas in masting appears to have largely gone uncommented (e.g. [7]).

136 A secondary, more specific, hypothesis can be framed as two alternatives. They are
137 not fully exclusive of one another though. (i) Ectomycorrhizas might achieve a form of
138 economy of scale due to extensively shared hyphal networks between the roots of large adult

trees [54], possibly also via root grafts, which could equilibrate levels of the limiting nutrient resource [55] and thereby lead to trees reaching similar internal thresholds simultaneously. (ii) Year-to-year stochasticity in climate [6, 56], especially seasonally-related rainfall, might cause soil nutrient availability and uptake to increase in the interval years between masting events, thus enabling stores to increase across all trees together. Here no economy of scale is necessary. These two processes could conceivably interact in a non-linear positive manner (extending [57]), enforcing common years of masting, because they both depend on ectomycorrhizas and rooting activity.

An ecosystem that can test the nutrient resource limitation hypothesis well would be high-stature primary forest, for which C is in abundant supply, on soils very low in one or two elements that are macronutrients. Such an opportunity was afforded as part of the long-term work in Korup National Park (SW Cameroon) since the 1970's. Supporting knowledge of masting tree growth, forest dynamics, nutrient cycling, soils and climate are laid out in the following Background section.

The present paper builds on the study of mast fruiting in *Microberlinia bisulcata* A. Chev. between 1989 and 2004 [10] and extends it to 2017 (29 years). In the 'Discussion' section, a synthesis of the new results, an improved hypothesis and schematic model are developed and integrated with a review of the literature.

Background

Forest ecosystem

Korup National Park, in the South-West Region of Cameroon, is covered by primary rain forest of the Atlantic Coastal type [58], and lies within the Guinea-Congolean refugium

162 [59]. Local and regional maps are found in Gartlan et al. [60] and Newbery et al. [61]: further
163 details of the site are given in Newbery and Gartlan [62] and Newbery et al. [10, 63].

164 *Microberlinia bisulcata* dominates large patches or 'groves', 1-3 km across, in the
165 primary rain forest of southern Korup. Trees ≥ 50 cm stem diameter attained 17.8% of the
166 overall density and 32.6% of total basal area in 2005, and together with co-dominants
167 *Tetraberlinia bisulcata* and *T. korupensis* correspondingly 46.5 and 61.3% [63, 64]. All three
168 species are strongly ectomycorrhizal as are several other co-occurring tree species of the
169 subfamily Detarioideae in the Fabaceae (formerly Caesalpiniaceae-Leguminosae; [61]). The
170 taxonomy follows the revision of LPWG [65] and de la Estrella [66]. They are not N-fixing
171 trees. *Microberlinia bisulcata* trees attain considerable stature in the main canopy,
172 characterized by wide dome-shaped crowns, and very extensive laterally-spreading buttress
173 systems [63, 67]. The species is a leaf-exchanger and therefore semi-deciduous: new leaves at
174 the start of the dry season (December to February) push off the old leaves, flowering follows
175 within a month [10, 55]. Flowers are outcrossed mainly by small bees and pollen seems
176 unlikely to be limiting: bees are highly abundant in the canopy during the dry season [55]. It
177 remains untested, however, whether insect pollination could form an economy-of-scale
178 factor: in this connection presumably density of trees plays a crucial role. Into the wet season
179 (March to October) pods mature from soft green to hard fibrous brown structures. Seeds are
180 dispersed ballistically in August-September [68].

181 The Korup-Ndian area along with Douala at the coast is climatologically special for
182 western Central Africa because it has one clear dry season each year as opposed to the two
183 less-distinct ones found elsewhere in the region. Mean annual rainfall 1984–2016 was 5159
184 mm (range 4023 to 6531 mm). The typical seasonal course in rainfall is shown in Newbery et
185 al. [69], with almost none in January and February but reaching to 900–1000 mm in August
186 or September. Site elevation is ~120 m a.s.l. (range 40 to 200 m from south to north inland),

slightly varying between swampy stream-fed lower areas up to local slopes, in places strewn with quartzite rocks. The soils are very sandy and free-draining, acidic and very low in available P and K [60], meaning that here high-stature tropical forest is growing on one of the most nutrient-poor sites in tropical Africa. Within groves, soil organic matter is largely confined to the top 2 cm of the profile, forming a surface mat that is densely occupied by fine roots and ectomycorrhizal hyphae [61, 69]. Larger vertical roots are able to tap deeper water reserves. Nutrient cycling in the groves shows a 'fast-forward' modus: leaf litter decay is fast, there is no permanent leaf litter layer, and most cycling via the very efficient mat happens in the early wet season [70, 71]. At this time throughfall nutrients help to prime decomposition and uptake [72]. For the rest of the year, heavy rains leach the forest, and this results in a tight closed ecosystem in which ectomycorrhizas play a central role in P acquisition and uptake [69]. In addition, annually in the dry season, Harmattan dusts bring some P to the forest by aerial deposition. A critical field experiment showed that growth and recruitment of *M. bisulcata* was not P-limited [73], possibly because of the highly evolved adaptations to the low P site or another element like K was limiting.

Recruitment of *M. bisulcata* over at least the last six decades has been poor due to very low seedling and sapling survival [55, 74-77]. Seed production in mast years is copious [10] but this species' seedlings are strongly shade-intolerant [78, 79]. The groves demonstrate transient dominance: the stands now are predominantly made up of large to very large trees, with extremely few small ones present [63]. The dynamics is thought to be one of patches arising and then decaying, being replaced, *in situ* or *ex situ*, within a mosaic of species-richer forest [62, 63]. The species is classified as a long-lived light-demanding tree (see [76]). Part of the expected life-history strategy of long-lived and light responsive species such as *M. bisulcata* would be to delay the size on maturity (SOM) in order that greater seed output later offsets the relatively low probability of persistence in the forest understorey. Two further

212 coevolved traits are the ectomycorrhizal habit mentioned and mast fruiting. Ectomycorrhizas
213 not only provide advantages in resource acquisition for juvenile and young adult trees but are
214 also thought to be a means to store resources which enable mast fruiting in the older adult
215 ones [10, 55]. A key sub-hypothesis has been that these links between adults synchronize the
216 timing of masts by equilibrating nutrient sinks across groves [55, 69]. There is increasing
217 evidence from other forests that ectomycorrhizas build intricate below-ground hyphal
218 networks between individual trees (e.g. [80, 81]), although the definite evidence for these
219 networks providing a means of C or mineral nutrient transfer is not consistent, at least for
220 adults to seedlings [82]. However, in the context of mast fruiting of adults, the hypothesized
221 transfers are between very large trees occurring in dense stands (the groves at Korup).

222 Mast fruiting

223 Mast fruiting in *M. bisulcata* was first realized from early phenological recording in
224 1988 to 1995, with prominent seed crops in 1989, 1992 and 1995 and barely any seed fall in
225 the intervening years [55]. Flowering occurs to some extent in most years (a few fail
226 completely); and not always does a heavy seed crop depend on heavy flowering [10]. The
227 two *Tetraberlinia* species tend to mast in the same years as *M. bisulcata* but not both together
228 ([55], and unpubl. data). After a propitious start with a potential 3-year cycle for masting (i.e.
229 a 2-year interval between mast years), this cycle turned out to be shorter later. Because
230 masting was associated with peaks in mean daily radiation in the dry season prior to fruiting
231 this suggested that C was at a premium, and some threshold needed to be crossed before
232 masting occurred. Detailed nutrient cycling studies in plots dominated by *M. bisulcata*
233 showed for the first time that leaf litter after a mast year (1989) was low in P concentration
234 compared with the years to either side, and this was matched by a decline available P in the
235 soil, especially in the surface organic layer [69]). This last result suggested that P was being

236 shunted into the seed crop and less was remaining to be shed in litter and, given the low soil P
237 at the site and the presence of ectomycorrhizas, P was also likely limiting mast fruiting. Tree
238 C and P levels might be operating a double-threshold control system and this led to the
239 phosphorus and climate proposed ectomycorrhizal response (PACER) hypothesis [69].

240 The climate at Korup varies stochastically from year to year, particularly regarding
241 the start, duration and intensity of the dry season (the dates defining the actual season each
242 year based on 30-day running rainfall total (*rft*) falling < 100 mm; [10]). This season plus the
243 first 6 weeks of the wet season very largely determine tree physiological processes for the
244 whole year. Fine-tuned sensing of the environment to optimize resource gain and allocation
245 within a life history strategy is central to survival. Under- or over-allocation at the wrong
246 time could lead to large fitness losses, hence the presumed operation of thresholds that safely
247 trigger phenological change. That C and P might be dual constraints within a broader
248 nutrient-limitation hypothesis as an explanation of mast fruiting for many tree species
249 required a detailed budget to show how much C and P (also N and K) were being allocated to
250 fruits and seeds in a main masting event. Censuses of seed and pod counts, their masses and
251 nutrient contents were achieved for the 1995 masting [83], showing that *M. bisulcata*
252 produced on average 26K seeds per tree or 83.5K seeds/ha. Seeds are small (0.64 g each), and
253 with an average of 2.0 seeds per pod, total pod mass was 25 g (see images in Appendix S1 of
254 [68]; at the 2007 and 2010 events 2.5 seeds per pod were estimated). Masting resulted in an
255 investment of 1034 kg /ha dry mass that year, and compared with leaf litter production in
256 previous non-mast years [70], was 52% of it by comparison, or in a mast year 74%, i.e. a
257 substantial allocation of resources [83]. Seeds and pods together had N and P amounts 13 and
258 21% of that in annual leaf litter production, indicating an important use of P during masting.
259 Unfortunately, C, P, N and K investments in flowers are unknown but if included they would

increase the reproductive allocation estimates slightly. Flowers of *Microberlinia* are very small in mass compared with seeds and fruits.

Using a detailed 150-tree phenological study in the main P-plot at Korup of 1995–2000, and incorporating circumstantial reliable observations in the field from previous and later years up to 2004, enabled a better picture of how dry season variability might control mast fruiting in *M. bisulcata* [10]. From daily rainfall and radiation data (recorded locally at Bulu, Ndian; 1984–2017), a clearer model was developed. Masting was tending to occur when the prior dry season was *drier* than average (more intense, low mean daily rainfall), plus the dry season in the year prior was *wetter* than average (less intense, high mean daily rainfall). After 1993, radiation did not show the same trend as in 1989–1992, largely because after 1995 it climbed steeply as part of an inferred 11-year solar cycle [10]. The relative change in radiation between successive years was important, and not the absolute levels. The notion that time series of the environmental variables at Korup were or ever had been stationary is hard to sustain.

The argument developed was that the current year's dry season dryness reflected also to some degree increased radiation, but the wetter dry season the year prior was possibly indicating better conditions promoting tree nutrient uptake at the most effective time. The detailed phenology data showed that masting was strongest on trees on upper slopes (i.e. sites with relatively drier surface soils in years with a 'dry' dry-season), and that in the moderately 'wet' dry season of 2000, those trees that masted were also on the drier sites. This tentatively pointed to surface soil moisture in the dry season being a key determinant to what was happening. The intensity of the dry season is unlikely to have particularly affected the water balance of adult trees themselves because they would have had access to deeper water sources: after all, trees flushed, leaves and branches grew, and flowering took place, in the dry season. Taken together, the preliminary evidence pointed to processes in the organic mat

regarding fine roots and ectomycorrhizas, coupled to nutrient transfers within the trees and ectomycorrhizal network [10, 52]. With the masting time series extended to 29 years—almost twice its previous length, plus information collated from several nutrient studies at the site, further tree phenology censuses, a more detailed statistical modelling of fruiting on rainfall and radiation, and the effects of an unexpected herbivore attack—this paper assesses the extent to which C, P and K, might be determining the masting cycle in *M. bisulcata* and, in extension, presents a more refined hypothesis and model of the phenomenon.

Methods

The research reported here was part of a collaboration between the Universities of Bern and Buea. The Ministries of Forests and Wildlife (MINFOF) and Scientific Research and Innovation (MINRESI) granted permission to conduct the research, and the Conservator's Office of Korup National Park approved access to the field site. Further information global research inclusivity is given in S1 Checklist.

Climate records

Climate data continued to be available from the PAMOL Bulu Station, Ndian [84]. The station lies 12 km to the SE of the study site. Daily radiation, rainfall and temperature were recorded since 1 January 1988 until 27 May 2017. Radiation was estimated using a Gunn-Bellani (BG) radiometer, with volume evaporated per day (V, ml) convertible into radiation (R, W m^{-2}). Two periods, however, lacked radiation data because of instrument failure in March–May 1993 and April 2009–May 2011. Improved new radiometer calibration equations were developed using several shorter series of pyrometer measurements and these applied to the complete time series to obtain mean monthly radiation (text in S1 Appendix).

The short break in radiometer readings had been previously linearly interpolated, but the radiometer data for the much longer break 2009–2011 required more refined statistical methods. These are outlined in the analysis in S1 Appendix. Since radiometers are rarely still in use today, this step in methodology is original. It also meant that the standard BG instrument calibration curve (used in [10]) could be replaced with the now much better site-specific parameters. The equations were applied to the whole series 1989–2017, with differences to the first half of the time series referenced in S1 Appendix. World Climate data bases unfortunately proved quite inadequate for estimating these missing values due to the sparseness of regional stations in western Central Africa and the special topography around Mt. Cameroon (SSE of Korup), with the few data records available for the last decades being incomplete (see S1 Appendix).

A dry season occurred when the 30-day running rainfall total (*rft*) at Ndian (Korup) was < 100 mm, and this gave a defined start date and duration (the 'drought-defined dry season' of [10]). This dry season typically moved one month back or forward around the modal months of December to February, coming earlier or later in different years, and often shorter or longer. Hence, in what follows, 'dry season 1991' for example means December 1990 to February 1991 (modally). For a more general, less strict, annual matching of phenology to climate, a 12-month year starting on 1 December one year and ending on 30 November the next was adopted, with quarter 1 being December to February, and so on. Part-years were taken as November to March (5 months, dry) versus April to October (7 months, wet) to encompass the weeks before and after the dry season proper. Since its use in Newbery et al. [10], the definition of drought dry season was slightly relaxed in that within the outer defining limits a very few days where *rft* was at < 103 mm were counted in as drought days as long as the total went back below 100 mm for the rest of the season. This affected four of the 16 years slightly in their dry season durations and mean daily rainfall values (Table 1).

Table 1. Incidence of mast fruiting in *Microberlina bisulcata* at Korup for the years 2005 through 2017, and dry-season climate variables (i.e., last dry season before the event). 'Year/dry season' denotes, for example, the dry season from end 2004 into early 2005, coming before the masting in 2005. 'M' indicates a strong pronounced masting, 'm' a modest but still significant one. This table is a direct continuation of Table 1 in Newbery et al. [10] for 1988–89 to 2003–04. The exception to note is the updated radiometer calibration equation applied (S1 Appendix) which changed the scale (linearly) for radiation. The new radiation values for 1989–2004 are also in S1 Appendix.

Year/dry season	Masting event	Start (days from 1.12)	Duration (days)	Mean daily rainfall (mm)	Mean daily radiation (W m^{-2})	Minimum temperature (ºC)
2004–05		20	65	1.55	148	18
2005–06		39	38	2.50	157	22
2006–07	M	12	85	1.01	152	19
2007–08[a]		47	50	1.71	158	19
2008–09		34	21	4.66	137	22
2009–10	M	4	58	1.42	152	22
2010–11		26	43	2.07	158	19
2011–12[b1]		21	48	1.95	163	21
2012–13	m	26	54	1.90	165	20
2013–14 [b2]	m	39	21	0.95	165	21
2014–15		32	47	2.22	173	20
2015–16	m	13	92	1.02	154	21
2016–17	m	26	83	2.19	167	22

[a] This dry season had a short break (running rainfall total went above 100 mm slightly) near its start.

[b] caterpillar attacks at the ([1]) start and end, or ([2]) middle, of these dry seasons.

Phenological recording

The main 'P-plot' is located in the southern part of the Park (5º10' N, 8º70' E; global coordinates 0476438/ 0553538) at an elevation of 96 m a.s.l. (see [63, 64] for further details). The incidence of mast fruiting from 1989 to 2004 has been reported and analysed in [10]. Recordings were extended anew from 2005 to 2017 for a subset of trees, and it is this full time series of 29 yr that is presented and analysed in the present paper.

Evidence for masting rested on a mix of intensive phenological scoring of marked trees in the two periods; quantitative trap-based estimates of seeding in two specific studies and from which masting fruiting was inferred; circumstantial records linked to within-stand field seedling experiments in some years, and general yet objective assessments of the whole forest in others in the course of conducting experimental studies (Table A in S2 Appendix). Following pod maturity to completion was not possible in 2017 because of security restrictions preventing further access to KNP. The situation remains unresolved as of early 2024.

To increase the frequency of recording, between 1995 and 2000, 150 *M. bisulcata* trees in the main 82.5 ha 'P-plot' (out of 294 in total with stem diameter ≥ 50 cm; [63] had been scored on 61 occasions (mostly at monthly intervals), for intensity of leaf fall, leaf flush, flowering and immature and mature pods (scale 0, none; 1, ~25; 2, ~50; and 3, ~75 and up to 100%; [10]). Later, within an 8-ha sub-area of the 82.5-ha P-plot (1000–1200 m E, and 100–500 N, with respect to SW origin; see Fig 2a of [63]), 61 of the 65 trees surviving since the last enumeration in 2005 (stem diameter, mean ± SE = 112 ± 4 cm, range = 54–174 cm), were scored between 2009 and 2013 in a similar manner as the first period. In 2014, fallen pod density on the ground was taken as a proxy for mature pod density (Table A in S2 Appendix).

Fig 2. Times series of the dry season climatic variables associated with the masting series. (a) mean daily rainfall; (b) mean daily radiation; (c) start date (from 1 December of year prior) and (d) duration of the season, i.e. that which preceded the masting event; (e) radiation intensity (= radiation x duration·10^{-3}); and (f) the difference in radiation ($radi_d$) between successive years (current minus prior). Symbol colours: brown, full; orange, partial; and green, no; masting event.

Masting was categorized as 'high' (labelled 'M') when all, or almost all (> ~85%), of the recorded trees had many pods, and 'moderate' ('m') when fewer trees (~45–85%) had many pods, or numbers of pods on relatively more trees were lower. These events were clearly differentiated from those with 'no' or 'very low' pod productions, and from those 'low' ones with just a few to several (~< 20%) trees masting (Table A in S2 Appendix). The masting scale was therefore semi-parametric. In the Results section later, three categories of event are used: 'M' and 'm' as masting; and the set "none, very low and low" as non-masting. Direct estimates of seed output as a quantitative measure of mast fruiting, or even qualitative crown scoring, for all trees in all years was simply not feasible at this remote and difficult field location.

Nutrient sampling

In an earlier litterfall study between May 1990 and June 1992, monthly bulked samples from twenty 40 x 40-cm traps in each of 10 subplots were divided into two halves as set A, for separation into fractions (leaves, small wood, etc.), and set B, for separation of just leaves into the commonest 26 species [70]. From this set B, leaves of *Microberlinia bisulcata* were selected and later — as for the other species — they were analyzed for N, P, Ca, K and Mg concentrations. Leaflets and rachises were kept together. As this species is a leaf-

388 exchanger, it has a very well-defined period of leaf litterfall each year, starting with onset of
389 the dry season [10]. Five subplots were in low (LEM) and five in high (HEM)
390 ectomycorrhizal stands (each 40 x 80 m) along the transect P in Korup [60, 69].
391 *Microberlinia bisulcata* occurred in only the HEM subplots, so the number of replicate
392 nutrient values per month was five. The 26 months were divided into seasons according to the
393 median rainfall pattern at Korup (as defined above), with those in the dry season being
394 generally December 1990–February 1991 and December 1991–February 1992, and the other
395 months the longer wet seasons. Only dry seasons are considered here, and nutrient
396 concentrations for them were averaged across the three constituent months. A mast fruiting
397 occurred in (August-September) 1989, so dry season 1990–1991 is the second dry season
398 after the event, and dry season 1991–1992 the third one. The next masting was in the wet
399 season of 1992, so seen from this perspective the two dry seasons sampled were ~ 6 and 18
400 months prior to the second event.

401 The opportunity to sample *M. bisulcata* leaf litter immediately after a later mast
402 fruiting came in the 2010–2011 dry season. A large system of over 400 seed traps had been
403 used to follow seed production and dispersal in the August-September 2010 masting [68].
404 These traps remained in place until early 2011 collecting leaf litter. The dry season had
405 started on 26 December 2010, and samples were taken on 29 January 2011. This interval of
406 ~1 month would have covered a very large proportion of the leaf fall of this species that year,
407 although the thin tail into February was not included. Thirty traps (from 68 small clusters of
408 the traps within 25 ha of the 82.5-ha permanent plot, [63]) had sufficient quantities of almost-
409 only *M. bisulcata* leaves, lying in the traps as a well-defined readily collectable upper layer.
410 Leaflets and rachises were separated on this occasion, and analyzed for the same five
411 elements as in 1990–1992, later recombining at the whole leaf level. The mean dry mass ratio
412 of leaflets to rachis in *M. bisulcata* leaves was 0.793:0.207, very close to 4-to-1.

413 In the dry season 1997–1998 four traps of galvanized metal (same as used in 1990–
414 1992) were compared with four similar ones but lined with hessian sacking (used in the
415 1989–1991 study of Newbery et al. [69], each set being placed at random in each of the two
416 quarter plots of six HEM half-plots. Litter was collected over four consecutive fortnights
417 between 21 December 1997 to 15 February 1998. *Microberlinia bisulcata* leaflets and
418 rachises were again sampled separately, dried and analyzed for N and P concentrations. Not
419 all traps had sufficient material and the replication per subplot/trap type/date ranged from 2 to
420 4. N and P values were successive averaged for trap type, then subplot, and their weighted
421 4:1 leaflet-rachis averages found for the 24 date x plot combinations. Trap type had no effect
422 on these two elements' litter concentrations (before tests for Zn contamination had been
423 made). This litterfall was collected midway between a moderate double masting in wet
424 seasons 1997 and 1998.

425 The 1998 masting event's seeds and pods, previously analyzed and reported in [83]
426 for N and P, were analyzed further for K, Mg and Ca using standard acid digest methods and
427 spectrometric determination (see e.g. [85]). To find the nutrient masses allocated to
428 reproduction (fruits) and to compare them to the same used in foliage, leaf litterfall values
429 from another similarly strong (1992) mast year were taken from Green and Newbery [83]. In
430 these new calculations, mature leaf concentrations (for N and P) were used from a
431 retranslocation study in Chuyong et al. [70], which involved three dates: viz. December 1991,
432 and April and July 1992. Litter fall dry mass very slightly underestimated mature leaf mass
433 because of element retranslocation during senescence. Essentially, these leaf concentrations
434 were from trees sampled on average 5 months before seed dispersal, and therefore concurrent
435 with pod maturity that year.

436 In a separate study of litterfall by Schwan [86], paired litter traps (same again as used
437 by [70]) were placed at random below the crowns of 20 *M. bisulcata* trees in the main P-plot.

The bulk of the litter (~90%) fell in the 3-week period of 9-30 December 2002. This 2002–2003 dry season came immediately after a masting in 2002, and next one was in 2004 [10]. In this study only leaflets were analyzed for N, P, K and Mg.

Soil moisture measurement

Soil moisture was recorded across two dry seasons to demonstrate that its variation could underpin soil nutrient processes which were affecting mast fruiting. *M. bisulcata* trees spread their extensive lateral fine root systems and ectomycorrhizas mainly in that drying soil surface layer [67, 69]. An additional aim was to determine by how much soil moisture content was reduced by rainfall deficit.

On 2 December 2003, 12 soil moisture content sensors (Theta Probes ML2, Delta-T Devices, Cambridge, UK) were installed in a stratified random manner across the eastern 30 ha of the P-plot, one per block of 100 m x 250 m. Each probe was inserted horizontally (at 40 cm depth, excepting three at 20 cm due to access problems) into a hole excavated at the side of a small pit, the latter backfilled and packed down to the original density. A subsample of soil from the excavated side hole was retained for fresh, water-saturated, and later oven-dry weight (105 deg. C). With a hand-held meter, soil moisture content (SMC, %) was recorded fortnightly until 26 April 2005 (38 times). Readings were repeated between 15 November 2006 and 15 March 2007 (nine times), with one last recording on 29 January 2011. In the years 2004 and 2007 *M. bisulcata* had major mast fruitings, in 2005 and 2011 it had none.

Results

Mast fruiting pattern

The extended time series shows that after 1995 there was a double year 1997–1998 with high seed crops, 1998 somewhat weaker than 1997, and then the interval dropped to 1 year (from a 3- to a 2-year cycle), with a masting sequence 2000, 2002, and 2004, returned to strong 'M' masts in 2007 and 2010 with a 2-year interval, and then after that the control seemingly weakened to result in two pairs of consecutive years, 2013–2014 and 2016–2017 which had moderate 'm' mast fruiting (Fig 1a). The time series as it extended began to show increasing non-stationarity (i.e. change in temporal pattern over time), the 3-year cycling of first period of 1989–1995 returned only once in 2004–2010: the regular cycle was seemingly temporarily disturbed. Nevertheless, 'on average' over the 29 years, and taking as markers the first of those pairs of years with partial masting (2013, 2016), there appears to be good evidence for an intrinsic 3-year cycle.

Fig 1. The time series of mast fruiting of *Microberlinia bisulcata* at Korup, 1989-2017. (a) The observed data. Symbol colours: brown, full; orange, partial; and green, no; masting event recorded. 'C' marks the year 2012, in the dry season of which the strong caterpillar attack occurred, and 'c' the one in 2014 which was a smaller more localized attack. (b, c) The probability of masting as fitted for 1989-2004 (squares), and predicted from 2005-2017 (triangles), using binomial logistic regressions of masting on the logarithm of rainfall in respectively the current and prior year's dry season. Symbol colours: brown, full; orange, partial; and green, no; masting event recorded.

Approach to the statistical analysis

The fitting of masting, as a 0/1 binomial response variable, to the climate variables was first limited to the 24-year period 1989–2012 because all the events were strong and pronounced ('M' in Table 1; Table A in S2 Appendix). Logistic regressions were run with dispersion (φ) either fixed at 1.0 or estimated [87]. Whilst the latter gave marginally more

484 significant fits, the former was adopted because the sample size was small and the estimation
485 of φ would be unreliable [88]. The binomial error distribution appeared to be satisfactory: the
486 complementary log-log one did not improve fitting. Simple logistic regression does not
487 account for temporal autocorrelation, however. With records for only ~60 trees in common
488 across all events, sample size was too small to apply Monte Carlo subsampling in order to
489 achieve temporal independence. Because of the non-stationary, randomization tests will not
490 provide valid inferences [89].

491 Extending the analysis to the full 29 years (1989–2017) required the ordinal, or
492 proportional-odds, logistic model [87, 90, 91], where 'm' (moderate masting) was scored as
493 0.5 (see Table A in S2 Appendix). Binomial and ordinal logistic models were run with the
494 'glm' and 'polr' commands in R ([92, 93], package 'MASS'; [94]), and in GenStat for
495 comparison where also φ could be estimated [95]. Given the modest length of the time series
496 and data set, different models were fitted mostly with single independent terms, and when
497 with two then the same variable with a 1-year lag, and only additively. No attempt was made
498 to search for a best-fit subset model with interactions; if fact, most such model fits failed to
499 converge when attempted.

500 Climate variation in time

501 Of the four basic climate variables, mean rainfall and radiation per day in the dry
502 season, and start and length of the season (current year of masting and year prior), only the
503 first required ln-transformation to remove positive skew along the independent variable axis.

504 Mean daily dry-season rainfall in years of full masting was lower than in those years'
505 prior with no masting (Fig 2a), with the exception of 2000, and if the averages of the rainfall
506 values for the two double partial masting years are taken these are on a par with the masting
507 ones. The time series for rainfall showed weak temporal autocorrelation (Fig C in S3

Appendix) and likewise, albeit a little more strongly, for ln(*rain*) at lag 1 (–0.293 vs. –0.221). (Note that the first correlation differs slightly from the rain versus $rain_{-1}$ one based on data which included the lagged 1988-value.) Radiation over time showed a distinctive pattern with a clear central peak between 1996 and 2005, then a rise again, apart from 2009, to those higher levels (Fig 2b): accordingly, the series evidenced non-stationarity, and as a consequence autocorrelation was positive and significant for lags of 1 and 2 years, then significantly negative ($P < 0.05$) for lags of 6–8 years (Fig C in S3 Appendix). The partial autocorrelation remained significant for a lag of 1 year only, however.

Start of the dry season varied around the third to fourth week of December with no clear patterns or differences between masting and non-masting years (Fig 2c), but it was negatively autocorrelated with a lag of 1 year, i.e. early starts tended to be followed by late ones, then early again, in successive years (Fig C in S3 Appendix). Excepting the two last years, duration of the dry season revealed a general decline (an approximate halving), those years with masting being often longer, and conversely of the six shortest-season years there was no masting, apart from 2014 which was partial (Fig 2d). Interesting, autocorrelation of duration was almost significant ($P < 0.05$) at a lag of 3 years (Fig C in S3 Appendix). Radiation intensity showed a very similar pattern to duration (since radiation varied much less than duration) (Fig 2e; and Fig C in S3 Appendix). Intensity of radiation in the dry season was expressed as mean daily radiation x duration. Lastly difference in radiation ($radi_d$) between successive years (one approach to removing trend and non-stationarity) was mixed with regard to masting response, although again a weakly significant negative autocorrelation for a lag of 1 year was evident (Fig 2f; and Fig C in S3 Appendix).

Modelling masting and climate

Binomial logistic regressions for 1989–2012 showed a significant negative effect of mean daily rainfall in the current year's dry season ($P < 0.05$), and a positive effect of mean daily rainfall in the dry season prior ($P < 0.05$), on masting. Using ln(*rain*) and ln($rain_{-1}$) improved the regressions fits with $P < 0.015$ (Table A in S4 Appendix). Mean daily rainfall was only weakly correlated with rainfall the year prior, untransformed values ($r = -0.190$, $P = 0.374$, transformed ($r = -0.272$, $P = 0.15$). This last result is important because a strong negative temporal autocorrelation, i.e. a year-to-year increase-decrease reversal, was absent. Regressions with both rainfall terms led to reduced fitting, because these coefficients were now partial ones adjusting for the correlation ($P = 0.093$ and 0.055). The same regressions with ln-transformed variables also changed the significance levels very little ($P < 0.10$; Table A in S4 Appendix). Ordinal logistic regressions improved the fitting further with the full 1989–2017 data. Concentrating on the models using ln-transformed variables, separate regressions were now more, and highly, significant ($P < 0.01$), coefficients with the same signs as for the binomial logistic ones (Table A and Fig A in S4 Appendix) and, whilst significance decreased again using two-term models, the fits were still relatively strongly significant overall ($P < 0.025$).

The mean difference in ln-transformed dry-season mean daily rainfall, ln(*rain*), between the current masting (t_0) and year prior (t_{-1}) was highly significant ($P < 0.005$), but much weaker for the same and penultimate year (t_{-2}) ($P = 0.15$). Back-transformed means were 1.37, 2.49 and 1.69 mm/day respectively (see Table B in S4 Appendix). Comparing rain at t_0 with means of *rain* at t_{-1} and t_{-2}—applying equal or unequal weighting—led to very similar results as those at t_{-1} alone ($P < 0.005$). As a robustness test of the strong vs moderate ('M'/'m')-grading of mast fruiting, and how that might have affected the relationship with mean daily rainfall in the dry season where there was some uncertainty in the final grading, 1989–2017 ordinal logistic regressions were rerun with 'M' for 1998 and 2000 replaced by

556 ‘m’, i.e. 1.0 by 0.5. The dependence of masting on ln(*rain*) in the current and prior seasons
557 became slightly stronger ($t = –3.209$, $P = 0.0036$; $t = 2.913$, $P = 0.0074$, respectively).

558 Mast fruiting showed no significant dependence on mean daily radiation in the
559 drought-defined dry season, for either the 1989–2012, or 1989–2017, time series (using
560 binomial and ordinal regression, respectively), for the current (*radi*; $P = 0.72$ and 0.80) or
561 prior ($radi_{-1}$; $P = 0.55$ and 0.62) seasons. Correspondingly, start date was also a poor
562 predictor of masting for the current (*start*; $P = 0.34$ and 0.29) or prior ($start_{-1}$; $P = 0.18$ and
563 0.27) seasons. Duration, although only weakly significant, was better for the current (*dur*; $P =$
564 0.080 and 0.095) or prior (dur_{-1}; $P = 0.071$ and 0.138) seasons. It is important to note here
565 that radiation values for the 2010 and 2011 dry seasons had been interpolated (S1 Appendix),
566 so model predictions for the 2010 masting event come with an additional level of uncertainty.
567 Masting was only marginally or non-significantly dependent on masting intensity in the
568 current and previous dry seasons (positively and negatively respectively; binomial logistic, P
569 $= 0.083$ and 0.097; ordinal logistic, $P = 0.096$ and 0.165). There is therefore some indication
570 that high intensity reduces the likelihood of masting in the following year. Differences in
571 mean daily radiation (current-minus-previous, $radi_d$), on the drought-defined dry-season
572 basis, had no clear effect on masting (binomial logistic, $P = 0.31$; ordinal logistic $P = 0.84$).

573 Radiation did show a long-term trend since the start of recording until 2017 (Fig B in
574 S3 Appendix), with the evident 11-year cycle. This was not related to change in
575 instrumentation at Bulu (S1 Appendix). Using a LOWESS regression fitting model in R
576 (‘lowess’ command—a set of local smoothing splines), this trend could be removed and the
577 differences between empirical measurements and the detrending curve then used as adjusted
578 local year-to-year changes (Fig B [a] in S3 Appendix). The best result was with a span
579 parameter of $f = 0.25$, which meant that radiation values > 1 year prior or ahead had some
580 weight in fitting values for any one year, which simple differences between successive years

did not. Binomial (1989–2012) and ordinal (1989–2017) logistic regression fits of masting to drought-defined dry-season *radi* and $radi_{-1}$ were, however, all clearly insignificant ($P = 0.34$ to 1.00).

Lastly, to check whether heavy showers early in the dry season may have damaged flowers or interfered with pollination success, mean daily rainfall was plotted across each year's season. Of the 14 years with strong ('M') or moderate ('m') mast fruiting, ten had no showers of ≥ 15 mm/day in the first 30 days, whilst in the 15 years without mast fruiting eight had no showers ($\chi^2 = 3.55$, df = 1, $P = 0.060$), suggesting only a marginal tendency for mast years not to have experienced potentially destructive rainfall events.

Taken together, these regression model fits suggest that only mean daily rainfall in the current and prior dry seasons was strongly affecting the odds of masting. The exponent of the coefficient (e^{β}) estimates the fold-change in odds of masting per unit increase in mean daily rainfall. Since the range in mean daily rainfall over the years was approximately 1 to 3 mm, this translates on the ln-scale to *c*. 1 unit, meaning that in the transformed-variable models the change in odds covers the range in rainfall. This outcome provides a sound basis for predicting future masting events.

Predicting masting from models

Using binomial logistic regressions of masting 1989–2004 on ln(*rain*) in the current and previous years, fitted models were used to predict masting in 2005–2017 (Fig 1), on the original response scale of 0 to 1 (π; [87]). The series started at 1989, not 1987 as used in Newbery et al. [10]; and autocorrelation was not incorporated (see 'Time series analysis' later though). The model fit for ln(*rain*) was good for the mast years 1989, 1992, 1995 and 1997 (marginal for 1998), and good for 2002 and 2004, but it wrongly indicated a mast in 1993 and missed the mast in 2000 (Fig 1b; fitted intercept [α] = 3.61 ± 1.80 and slope [β] = –5.77 ±

2.62, $t = -2.206$, $P = 0.027$). Predictions of masting in 2007 and 2010 were very high (π = 0.97 and 0.83 respectively), and also that it did not occur in the intervening years. After 2012 though, one each of the pairs of moderate ('m') masts was predicted as full ('M', $\pi = 0.98$ and 0.97). The predicted masting in 2005 ($\pi = 0.75$) was incorrect, however.

With the model fit for ln($rain_{-1}$), 1992, 1995, 1997, 2000 [cf. with ln(*rain*)], 2002 and 2004 were all well-fitting as mast years, but 1989 and 1998 were not: 2001 was fitted as a mast year wrongly (Fig 1c; fitted $\alpha = -2.47 \pm 1.40$ and $\beta = 3.96 \pm 2.00$, $t = -1.98$, $P = 0.027$). Again, the model exactly predicted the mast years 2007 and 2010 masts ($\pi = 0.76$ and 0.97 respectively), and it managed three of the four 'm' (moderate) years afterwards as being moderate masts reasonably correctly. Therefore, similar to the outcome for cycles and intervals in mast fruiting, the model fits were fair-to-good up to 2012 (the caterpillar-outbreak year; see later subsection) but after that disorder and unpredictability ensued. Binomial logistic regression fits made with the 1989–2012 data gave predictions (not shown) that were very similar to those for 1989–2004, in the main because the mastings in 2007 and 2010 matched so well the time series to 2004: yearly π-values (fitted and predicted) from the two runs were in very good agreement.

The median effective level of ln(*rain*), that is the level when π (x) = 0.5 (defined as $x = -\alpha/\beta$; [87]) was 0.624, which back-transformed to 1.869 mm/day — a value very close to the estimate for the ln($rain_{-1}$) estimate of 1.867 mm/day. This median level, which might be interpreted as a form of threshold for non-masting and masting, applied well to the events and their rainfall values in most years up to 2011 (Table 1, Fig 2a) although ln(*rain*) and ln($rain_{-1}$) differed in a few years as being better or worse fitting and predicted. Years 2012, 2013 and 2014 had moderately high and quite similar mean rainfall in their dry seasons (1.90–2.07 mm/day; Table 1) so aside from the caterpillar intervention, the rain threshold theory would not have been expected to work too well—a form of counterfactual evidence. Afterwards, in

2014–2017, the return to low–high alternations in rainfall should, *ceteris paribus*, have led to 'M' (strong) masting in 2014 and 2017 (as predicted by the binomial logistic regression for ln(*rain*) (Fig 1b), but it still did not achieve that outcome.

Time series modelling

Times-series logistic regression—in full, generalized logistic autoregressive moving-average regression, with the command 'glarma' (R package glarma, [96]), accounts for temporal autocorrelations in binomial data [89, 97-101]. Its application here supported the binomial logistic regression results for 1987–2012 even more strongly ($P < 0.01$ and $P < 0.05$ for ln(*rain*) and ln($rain_{-1}$) respectively, for both lags p = 1 and 2, (Table A in S4 Appendix). Regressions using the time-series logistic regression model for *radi*, $radi_{-1}$, *start* and $start_{-1}$ either failed to converge or the fits were insignificant ($P = 0.17$ to 0.73). Whilst there was a weak positive effect on masting for duration in the current year ($\beta = 0.041 \pm 0.025$, $z = 1.64$, $P = 0.10$), an even stronger negative effect of duration was evidenced for the year prior ($duration_{-1}$; $\beta = -0.099 \pm 0.038$, $z = -2.62$, $P = 0.0087$) (Fig B in S4 Appendix). The last relationship analyzed before with a binomial logistic model was only marginally significant ($P = 0.073$) so the evidence for the effect improved.

The dependence of mast fruiting on dry season rainfall appears to be limited to the current and previous (t_{-1}) years, because repeat runs replacing $rain_{-1}$ with $rain_{-2}$, the mean daily rainfall in the second year prior to the current one (t_{-2}), were all clearly insignificant ($P = 0.39$ and 0.40) for 1989–2012 binomial logistic regressions, rainfall ln-transformed, single and two-term models respectively; and they were correspondingly insignificant ($P = 0.35$ and 0.76) for the 1989–2017 series with ordinal logistic regression. Moreover, dry-season rainfall at t_{-2} was poorly correlated with the same in the current year ($r = 0.027$ and 0.110), but slightly better with that at t_{-1} ($r = -0.187$ and -0.257). Time-series logistic regression fits did

not improve fitting to intensity of radiation (current or prior), differences in dry season radiation in successive years, or smoothed radiation regression residuals (current or prior) (P = 0.094, 0.062, 0.25, 0.74 and 0.26; respectively). Finally, masting was unrelated to minimum temperature in the current year's dry season (1989–2012, Table 1; binomial logistic P = 0.18; and 1989–2017, ordinal logistic P = 0.24).

Extending models for radiation

Whilst a rainfall deficit delimitation will define the drought period in terms of limited water availability, it may not necessarily correspond precisely to times of heightened radiation. Returning to the modal definition of dry season, namely the calendar months December through February (DJF), or first quarter of the phenologically referenced year, mean daily radiation can likewise be found (Fig A in S3 Appendix). Masting was not strongly related using binomial, ordinal or time-series logistic regressions, to this quarter's radiation however, in either the current or prior year ($P \geq 0.18$; Table C[a] in S4 Appendix), and also not for the other three quarters (Fig A in S3 Appendix; $P > 0.4$; model fits not shown). By contrast, and surprisingly, masting was strongly dependent on the *difference* in radiation, both in absolute ($radi_d$) and percent change ($radi_{d\%}$) terms, from prior to current year, and with all three regression models (P = 0.007 to 0.024; Table C[a] and Fig C in S4 Appendix; and Fig A in S3 Appendix). Using again LOWESS smoothing regressions to remove trend in radiation (Fig B[b] in S3 Appendix), with binomial logistic regression (1989–2012) masting weakly positively depended on differences in *radi* (P = 0.051) and negatively, though more marginally, for $radi_{-1}$ ($P < 0.1$) (Fig C and Table C[b] in S4 Appendix). Time-series logistic regressions improved the fits especially for *radi* ($P < 0.02$), although only slightly for $radi_{-1}$ (P = 0.08). Fits to detrended differences (1989–2017) with ordinal logistic regression were intermediate in significance to those with binomial and time-series logistic ones (Table C[b]

in S4 Appendix). Overall, there is moderate to strong evidence that the larger the increase in radiation between successive years, or the more positive the difference from the trend, the more likely a mast fruiting. This difference effect was not obvious in the earlier analyses of Newbery et al. [10].

An interesting feature of the LOWESS fits (Fig B in S3 Appendix), when taking radiation according to the two definitions of dry season, is how the outliers changed in relation to the smoothed curves. In the drought-defined case, 2001 and 2003 (both 1 year before masting) were very high, and 2006 and 2009 (also both 1 year before masting) were very low. Changing to the DJF-defined case brought 2001 and 2009 radiation much closer to the curve, and the binomial and time-series regression fits were improvements. Further, the autocorrelation was notably stronger, positive and significant, at lags of 1 and 2 years for this DJF-defined dry season than the drought-defined one, shifting to a significant negative correlation at an 8-year lag (Fig D in S3 Appendix). The partial correlation, again, remained significant for just the lag of 1 year. In the third (JJA) and fourth (SON) quarters a similar but slightly weaker pattern for the function occurred, the negative lag now at 10–12 years (Fig D in S3 Appendix). More interesting, however, was the almost unstructured weak pattern of the function for the second (MAM) quarter, that is no temporal autocorrelation over the early wet seasons (Fig D in S3 Appendix). Difference in radiation was significant for a lag of 3 years, and remained almost so for partial correlation, hinting at the 3-year cycle.

Start and duration of dry season reconsidered

To shed some light on the apparent paradox of the different definitions of dry season determining the relationship between masting and radiation, regression models were rerun with an extended dry season of the months of November through to March. All binomial logistic model fits, 1989-2012, using radiation in the current and prior dry seasons on this

new basis were clearly insignificant (P = 0.27 and 0.69). However, dependence of masting on $radi_d$ was marginally significant at P = 0.071 ($radi_{d\%}$, P = 0.052), and correspondingly so was it for the time-series logistic model with p = 2 (P = 0.056 and 0.043). Compared with the fits for the models using DJF as dry season (Table B[a] in S4 Appendix), these results for the 5-month season were weaker, suggesting that the influence of radiation was being diluted by inclusion of the additional 2 months; and this was reflecting the early wet season autocorrelation. Comparing radiation defined by DJF and that defined by the drought dry season graphically, both for differences between successive years and as residuals from the smoother curve over time (Fig D in S4 Appendix), indicated that a majority of the years lying above the 1:1 reference line were ones with masting and most of those below were non-masting, attesting that raised radiation differences and deviations were associated with mast fruiting.

The placing of start and end dates of the dry season was evidently critical to the analysis outcome because the degree of overlap between the two types of dry season were very variable from year to year (Table 1, Fig 1a). Mean, standard deviations and ranges in absolute differences were actually larger and wider for the drought- than DJF-defined dry periods (1.41 ± 11.14 [–21.0 - 21.1] and 0.72 ± 9.62 [–15.0 - 16.2] respectively). Even so, the reasons for the considerable overlap could be various because start and end dates of the drought-defined dry season were often very different from those of the DJF one.

When the mean daily radiation of the non-overlapping weeks with DJF increased or decreased, or vice versa, the $radi_{d\%}$ altered between successive seasons. Since masting fitted to $radi_d$ much better for the DJF- than drought-defined seasons, this would suggest that (a) radiation levels outside of the DJF months were most likely important, and (b) DJF-defined seasons allowed a more consistent year-to-year comparison than the drought-defined ones. That rain may have been lacking which defined the duration of the drought-defined season,

did not also imply radiation was changing proportionally. Radiation could have been sometimes high in the day and rain fell at night: conversely radiation could have been low when there was cloud cover and yet no rain, as was the case in some years at the transition to the wet season. Differences in successive years' dry season radiation were more, respectively less, pronounced in the first and second halves of the time series, for the DJF- than the drought-defined dry seasons.

Soil moisture content in dry season

On graphing the time series for 2003–2005, three of the 12 sensors had three anomalous and coinciding high peaks (~ 40 - <60%) in the 2004 and 2005 early-to-mid wet seasons suggesting that their locations were prone to flooding. These sensors' data for the whole period were accordingly omitted. Two of them were actually destroyed later by hunters. The time series of mean SMC is shown in Fig 3: it included the two dry seasons of 2004 and 2005, defined as before as when *rft* fell < 100 mm. Mean SMC over the 1.4 years was 16.80 ± 0.48%. Repeated measures analysis of variance for six times within each of the two dry seasons (Fig 3), using all 12 sensors' values, indicated that differences in mean SMC at the 20-and 40-cm depths were very small and insignificant: 10.98 vs 10.69% in 2003–2004 and 16.20 vs 15.89% in 2004-05, $P = 0.88$ and 0.89 respectively, df = 1,10). In a similar-length period in the late wet season 2004, starting soon after the peaked occurrences that year, a small difference was evident but again it was clearly not significant (20.20 vs 18.13%, df = 1, 10; $P = 0.39$). Interactions between depth and time were all insignificant for all three short periods ($P = 0.19$ to 0.36).

Fig 3. The course of soil moisture content (SMC, %), shown as means and SEs, at (mostly) 40 cm depth, for 2003-2005 at Korup. The horizontal red lines indicate the span of the dry season for each year (see also Fig A in S5 Appendix).

After the strong dry season of 2003–2004, during which SMC reached a minimum of 10.4%, its values remained fairly constant at 18.24 ± 0.31%. The dry season of 2004–2005 had much less influence on SMC (Fig 3). The lowest SMC-values in 2004 coincided with the lowest *rft*-values (down to 12 mm then 0 mm over 4 weeks); in 2005 SMC either did not go so low or remain low for long, and the match with SMC was weaker. At the start of the 2003–2005 series, the means (± SE) of SMC recorded and those found by gravimetric analysis were 15.09 ± 0.52 and 15.50 ± 0.82% respectively. The estimates were positively correlated ($r = 0.677$, df = 10, $P = 0.016$). Saturated water holding capacity was on average 38.15 ± 1.16%, less than the SMC at the peak times confirming that some locations were not always free-draining.

Between 2 December 2003 and 26 April 2005, SMC was related to 30-day running rainfall total as follows: SMC = 14.4 + 0.0070·rft ($R^2_{adj} = 40.5$ %, $F_{1,36} = 26.18$, $P < 0.001$, $n = 38$), inferring 14.4 % at 0 mm, and 21.4% at 1000 mm — the last *rft*-value being close to the June 2004 maximum of 995 mm. The difference in SMC between the very driest and wettest times of the mast year was therefore only 7% — for those locations assumed free-draining. SMC before the dry season of 2006–2007 was 20.7 ± 0.10%, and declined sharply and almost linearly to 14.0 ± 0.67% ($n = 9$ sensors), a difference of 6.7%. With the dry season that year lying within the span of SMC recording dates, this last value was likely very close, if not at, the 2007 SMC minimum. The mean value at 29 January 2011, a date also well into that year's dry season was 16.2 ± 0.8% ($n = 8$, one sensor lost because its cable was chewed), a value close to that in the dry season of 2005 (Fig 3).

The 30-day running rainfall total, *rft*, used to define the dry season in terms of drought when this total goes below 100 mm, does not indicate either how much is the deficit, or how

steep is the decline into, or incline out of, the dry season. Fig A in S5 Appendix shows the course of *rft* as the daily rainfall events occurred. The intense dry season of 2003–2004 (2004 was a masting year) resulted of *rft* going to zero, or very close to zero, for about 6 weeks (Fig A[b] in S5 Appendix), while in 2004–2005 (2005 was a non-mast year) it was near zero for perhaps just 2 weeks, and shorter overall (Fig A[c] in S5 Appendix). In 2002–2003, for comparison, the also long dry season *rft* reached zero for a couple of days, and whilst many days had no rain the season was broken by three high rainfall events keeping *rft* just below 100 mm (Fig A[a] in S5 Appendix). The relatively small decrease in mean daily rainfall between 2005 and 2004 (Fig 2) translated into a surprisingly large difference towards the lowered SMC and suggested a non-linear effect, that is a little less rain led to proportionally much more soil drying when rainfall was low-to-average.

Caterpillar outbreaks on trees

Chance attacks by herbivores offer good opportunities to assess how loss of foliage, and hence photosynthetic activity, could interfere with tree reproduction. In the latter half of December 2011, and again in the first half of March 2012, an outbreak of a black caterpillar was observed that fed on young foliage of *M. bisulcata* trees recorded for phenology in the P-plot. Although not quantitatively measured, the attacks were extensive, as evinced by the substantial amounts of falling frass, numerous caterpillars hanging below the crowns on threads, and litterfall consisting of soft, green leaf tissues (G. A. Neba and S. Njibili, pers. obs.). The same caterpillar was also recorded at another *M. bisulcata* grove 4.2 km due south, in March 2012 [102]. However, no visit was made to that site in December 2011. Fallen caterpillars were also observed feeding on young leaves of *Oubanguia alata*, a common understorey tree growing below *M. bisulcata* crowns at Korup.

Also in the latter half of December, but in 2008, an outbreak of most likely the same caterpillar species (an *Achaea* sp., probably *A. catocaloides*) had been recorded on *T. korupensis* trees in the same P-plot [102]. At that time, feeding upon *M. bisulcata* foliage was limited to low levels on just those crowns closely adjacent to the more heavily attacked ones of *T. korupensis*. Furthermore, and separately, at the end of January 2014 a morphologically different and larger species of caterpillar, yellow-green and behaving very differently from the smaller black one, was seen on five of the 65 monitored *M. bisulcata* trees (text and Fig A in S6 Appendix). Most probably it was another *Achaea* species. Intriguingly, this caterpillar species was feeding on *M. bisulcata* flowers, not young foliage. How influential the new insect herbivore was for *M. bisulcata* phenology that year is uncertain because its distribution was localized to a 2–3-ha patch where the *M. bisulcata* basal area was high.

Tree phenology and masting intensity

Tree phenology of *M. bisulcata* was compared between the heavy mast fruiting year of 2010, and the year of 2012 in which fruiting was very low (Fig 4; Table A in S2 Appendix). Both time series covered the drought-defined dry season of that year, and followed changes in leaf-flush and leaf-fall (leaf exchange), and flowering, pod formation (green) and pod maturity (brown). Attaining continuous fortnightly scoring was not always feasible and each series has two gaps. Leaf flush likely began a little before the start of the time series recorded for 2010, i.e. earlier than December 2009 (Fig 4a), but was adequately captured for 2012 (Fig 4b). The bulk of the leaf-flush happened within each year's dry season, flowering well within it in 2010 but coming at the end in 2012. Even though the sum of the flowering scores was similar in both years, pollination resulted in substantially more green and brown bods in 2010 than 2012 (Fig 4a, b). Caterpillars were not seen in the other years between 2009 and 2013, notably not in 2010. In 2010, green pods were apparent

822 between 18 January and 3 July, that is for 5.5 months, with a 1-month overlap as they turned
823 brown between 5 June and 28 August, over 2.5 months (Fig 4a). A similar time course was
824 recorded in 2004, and likewise (for green plus brown) in 1995 and 2000 (Fig 4b of Newbery
825 et al. [10]). Interestingly the overall period of pod formation was much shorter in the two
826 back-back years of masting 1997 and 1998.

827 **Fig 4. Changes in the mean scores of five phenological stages of *M. bisulcata* trees at**
828 **Korup in (a) 2009-2010 and (b) 2011-2012.** Stages: leaf fall (blue), leaf flush (purple),
829 flowering (green); immature (yellow) and mature (red) pods. The horizontal red lines indicate
830 the span of the dry season for each year (see also Fig B in S5 Appendix). Dates of caterpillar
831 attacks indicated with 'C'.

832 Trees in 2012 suffered unusually in two definite caterpillar attacks by the same black
833 *Achaea* species, both coming just prior to peaks in leaf-flush (marked 'C' in Figs 1a and 4).
834 The earlier flush in early January 2012 was part of the annual leaf exchange process, but the
835 later one in early April 2012 not. The first was in part associated with the leaf fall around 15
836 January 2012: 21 of the 61 trees lost new leaves then. The third leaf flush in late February
837 2012 (Fig 4b) had no associated caterpillar attack. What happened in late March was
838 unfortunately not recorded, but a building up of the re-flush starting then could be surmised if
839 this event followed the same flushing patterns of the earlier and later ones. The sequence of
840 events suggests that leaf flush in early January enabled the caterpillar population to initially
841 increase, and that at the end of February there was a response by the trees to the first attack.
842 The flush at the end of April is more difficult to explain. It could have been either a further
843 delayed response to the first attack, or a direct response to the second attack, by a possibly
844 now larger caterpillar population. The life-cycle dynamics of the herbivore would have
845 allowed, however, only a second cohort of caterpillars to feed on that third and last flush for
846 the year. The most flowering accompanied the middle leaf-flush peak in 2012, which speaks

847 against caterpillars being around then because feeding on leaves might be expected to
848 indirectly reduce flowering.

849 The presence of the black caterpillar in 2012 appears to have upset the smooth
850 phenological stage-replacement of 2010, and led to a much reduced reproductive output. The
851 interval from the last year of full masting (1 year) was theoretically suboptimal, so likely the
852 resource levels of P but not N were reduced and still below a threshold. A high N: P ratio
853 may have helped the caterpillar outbreak. In addition, the masting pattern changed after 2011
854 (Fig 1a), to the two moderate double-year form, possibly a carryover of the disruption of the
855 feeding in 2012, and a destabilization of the proposed inherent 3-year cycle. In the dry season
856 2010, mean daily rainfall was 1.42 mm, yet the year prior it was 4.66 mm; correspondingly
857 the rainfall for 2012 were 1.95 and 2.07 mm: prior-to-current ratios of 3.3 and 1.1
858 respectively. Interestingly, the lower caterpillar activity noted in the other grove to the south
859 was associated with average green-pod score of 1.7 in May 2013 (n = 33 trees; Table A in S2
860 Appendix), showing that masting was more intense there than in the P-plot that year.

861 The second herbivore attack in January 2014 of the other unknown caterpillar species
862 was before the second of the moderate 'm' mast fruitings of the double-years 2013–2014.
863 Much less is known about its effects particularly because detailed phenological recording did
864 not continue to end 2014. However, given that this species eats flowers, as well as young
865 leaves (S6 Appendix) it most likely reduced the number of trees able to fruit that year, even if
866 the outbreak was contained to a far smaller known area than the successive outbreaks of the
867 black caterpillar in late December 2011 and early March 2012.

868 It is instructive, once again, to look at the course of rainfall events and *rft* during and
869 immediately after the dry seasons of 2009–2010 and 2011–2012 to find clues for the second,
870 early March, caterpillar attack. This last came during a second short dry period when there

was that unusual third leaf flush (cf. Fig 4b with Fig B[c] in S5 Appendix). With an interval of ca. 14 days between phenology census recordings, it is difficult to say which came first; but the most likely explanation is the further dry period caused flushing and this promoted renewed feeding, possibly from a next cohort of caterpillars that year. The dry season 2009–2010 had also several dry days at a similar time but was broken by a large wetting event (and there was no further flush after the dry season one). For comparison, the pattern of 2010–2012 shows the shorter, later-starting and not so intense, dry season for a typical non-masting year (Fig B[b] in S5 Appendix).

Tree size-fruiting relationship

Consistency in the intensity of masting over time at the individual tree level was tested in the following way. Scores for brown pods in 2007 and 2010 were matched with those for an equally strong masting in 1995 on a tree-by-tree basis. Score categories '0' and '1' were combined. Fruiting was significantly positively associated in both cases ($\chi^2 = 10.61$, df = 1, $P = 0.031$ and $\chi^2 = 10.28$, df = 1, $P = 0.036$, respectively). There is good evidence that high- and low-scored trees tended to remain as such over a 12–15-year period, although considerable between-trees variability existed.

Ordinal logistic regressions of brown pod scores per tree versus tree stem diameter (at last census in 2005), in 2010, 2012 and 2013, or as fallen pods in 2014, were weakly and insignificantly related though ($t = 1.40$, 0.45, –0.68 and 0.42, e.d.f. = 58 to 61, $P = 0.17$ to 0.60). As the phenology score was recording the *relative* proportion of a crown fruiting, this means that large trees did not have proportionally more pods than smaller ones.

Oil palm yield comparison

Access to fruit yield data for oil palm (*Elaeis guineensis*) growing in the estates of PAMOL Plc on the eastern border of the KNP (Bulu-Mundemba, Ndian) allowed a comparison with *M. bisulcata* mast fruiting under the same local climate conditions. An analysis of the monthly yields, for 2003 to 2016, showed no year-to-year differences in means attributable to changes in either rainfall or radiation, although there was a very clear repeating pattern for each of the three variables within each year (text and Fig A in S7 Appendix). Moreover, mast fruiting of *M. bisulcata* in this period (see Fig 1a again) did not correspond to peaks or lows in this proxy measure of productivity, for either the current or prior year.

The poor relationship with radiation also means that yield cannot be used in an inverse estimation to confirm the interpolated missing months of radiation at Bulu in 2009–2011 (S1 Appendix). The Ndian estates have the same substrate and soil type as southern Korup. After initial trials in the 1960s through to the late 1970s, phosphate fertilization was discontinued because little beneficial effect on palm fruit production was found (C. E. Etta, unpubl. data). It is unlikely that much of the added P was still available in the soil by 2003.

Stem increment growth and masting

Annual radial increments (*incr*, mm) in stem growth of 20 cored *M. bisulcata* trees ≥ 50 cm diameter in the P-plot (see [63]) were matched to occurrences of masting over the 15 years of 1989–2003 (Fig A[a] in S8 Appendix). The end date was the last year which had a reliably-determined annual band for all trees. Standard deviation increased linearly with the mean over years (slope [CV] = 1.14, adj. R^2 = 50%, P = 0.002), indicating a considerable variability in increment between trees in any one year (Fig A[b] in S8 Appendix). No masting was noted for 1988 [69] but that is not fully certain.

Linear mixed-effects models were run using ln(*incr*) as the response variable, trees as subjects (or 'blocks') and ± 'M' as the factor. A binomial logistic regression fit of masting versus increment was not feasible as the power, with only seven events in the period, was low. There were no significant differences for increment in either the current year ($F = 0.79$, df = 1, 279; $P = 0.38$), or in the year prior ($F = 0.12$, df = 1, 279, $P = 0.72$: increments available for 1988), or in the year after ($F = 1.90$, df = 1, 259, $P = 0.17$). Thus larger respectively smaller increments were not associated with current mast fruiting, not (by inference) caused by it beforehand, or conversely masting did not cause a change in increment afterwards. Graphs of the increment series for each of 20 trees individually (not shown) had no common correspondences with 'M' years, and the differences in mean individual tree increment for fruiting type were highly inconsistent (+M: mean 2.49 ± SD 1.97, –M: 2.38 ± 1.98; differences 0.11 ± 0.77, range = –2.02 to 1.67). Mast fruiting appeared little connected to stem growth increment in *M. bisulcata*.

Increment was positively correlated, however, with mean daily radiation in the typically modal dry season period (using all records, i.e. 1984–2003), this 'quarter 1' being defined by months DJF – ($r = 0.507$, df =18, $P = 0.023$), but not in the early and mid-wet season quarters 2 and 3 ($P = 0.32$ and 0.41), although again in late wet season 'quarter 4' it was ($r = 0.479$, $P = 0.033$). Fruiting would have been largely 50% over then, by mid-September. For the year as a whole the correlation was also reasonably strong ($r = 0.503$, $P = 0.024$). Increment was not strongly correlated with rainfall in any quarter, nor overall ($P = 0.12$ to 0.70), and not with radiation in the year prior to masting ($P = 0.10$ to 0.73).

Binomial logistic regression fits of masting for 1989–2003 to mean annual core increment with either *radi* or $radi_{sr}$ (current or prior year for both variables) were all insignificant for the increment term (current: $P = 0.49$ to 0.63; prior: $P = 0.46$ to 0.95). The same approach applied using increment of the year prior brought little improvement in fitting

941 (P = 0.18 to 0.33; P = 0.18 to 0.62, respectively). Thus whilst increment and dry-season
942 radiation remained significantly positively correlated (r = 0.532, df = 13, P = 0.041),
943 partialling out a radiation effect was of little avail in unravelling a fruiting-stem growth
944 interaction.

945 Nutrients during the masting cycle

946 The newly-reported nutrient data, coming from the approaches described in the
947 'Methods' section above, are combined here with other nutrient data already published. To
948 begin with, for 1997 and 1998, and for 2011, the leaflet-to-rachis ratio of N was 1.568 and
949 1.524, and correspondingly for P it was 1.344 and 1.274 respectively, with means of 1.546
950 and 1.309. For 2011 only, the L/R ratios for K and Mg were 0.540 and 1.686. It was striking
951 how much higher was the K concentration in the rachises compared to leaflets.

952 In the 1990–1992 litter sampling the bulked samples each represented 0.320 ha of
953 forest. In 2011 sampling the trap clusters represented on average 0.368 ha. This means that
954 each nutrient value is similarly based on ~ 1/3 of a hectare, and the respective samples sizes
955 of 5-and-5 versus 30 can be retained in statistical comparisons without needing to group the
956 2011 ones. Likewise, the 1997–1998 study used some of the same half-plots, and accordingly
957 had the same scale as in 1990–1992. Working with the typical masting cycle of 3 years
958 shown by *M. bisulcata* at Korup over the period 1989–2010 [10, 55], the three sampling dates
959 together allow a series of immediately-after (2010–2011), and 1 (1990–1991) and 2 (1991–
960 1992) years after (and thus also immediately before the next), masting events to be
961 constructed. The two consecutive years are likely temporally correlated, but the time
962 difference between them and 2011 is large. The further data from 1997–1998 present an
963 interesting comparison in that masting in 1997 had evidently not prevented a repeat even the

964 following year. Over the successive four fortnights, concentrations of N were 18.69, 17.20,
965 18.58 and 18.63 mg g^{-1}, and those of P were 0.802, 0.799, 0.787, 0.956 mg g^{-1}.

966 The concentrations across the three weekly litter samples in December 2002 [86],
967 were averaged per trap. To obtain whole-leaf concentrations, the averaged values per tree
968 were first divided by the 1997–1998/2011 leaflet-to-rachis ratios to have indirect rachis
969 estimates, and then the 4:1 leaflet-to-rachis mass ratio was applied. This assumed that the
970 ratios from the 1997–1998 and 2011 studies could be used here for 2002 (which lay between
971 them). For the complete five-element data sets and direct estimation of leaf concentrations in
972 Table 2 (viz. 1991–1992 and 2011), years 1-3 after masting, N, P, K and Mg all differed
973 strongly and significantly (F = 13.4, 12.2, 27.2 and 6.01, all $P < 0.01$) but not Ca (F = 1.0, P
974 > 0.05).

975 The results show that in the inter-mast period, N was low for the first two dry seasons
976 and then rose the year before the next masting, P increased from low to high approximately
977 linearly in the period, Ca barely changed, K and Mg were relatively high for the first two

978 **Table 2. Mean (± se) concentrations (mg g^{-1}) of the macro-elements in leaf litterfall of *Microberlinia bisulcata*.** Collected were made in the dry season

979 immediately following the mast fruiting of 2010, and in the second and third seasons following the earlier masting of 1989 (t). NA = no data available.

$t_{>mast}$ (n)	year	N	P	Ca	K	Mg
1 (30)	2011	16.06 ± 0.25	0.597 ± 0.018	14.71 ± 0.58	4.41 ± 0.11	3.40 ± 0.13
1 (20)	2002[a]	17.39 ± 0.33	0.632 ± 0.026	NA	5.58 ± 0.45	3.43 ± 0.17
2 (5)	1991[b]	15.72 ± 0.66	0.692 ± 0.025	13.99 ± 0.82	4.67 ± 0.23	3.89 ± 0.17
3 (5)	1992[b]	19.33 ± 0.55	0.809 ± 0.047	12.70 ± 0.90	2.44 ± 0.07	2.53 ± 0.09
< 1 (6)	1998	18.27 ± 0.64	0.836 ± 0.057	NA	NA	NA

980

981 [a], Schwan [86]; [b], Chuyong [103] and Chuyong et al. [70].

982 seasons but fell in the third before masting (Table 2). This suggest that N and especially P
983 concentrations were depleted by the last mast fruiting and were re-instated before the next
984 event. K and Mg increased earlier in the interval but were presumably deployed elsewhere
985 before masting. Despite the different sampling approaches, standard errors of means, across
986 years per element, were quite similar. The concentration within the double-masting period
987 1997–1998 intriguingly lay between the 1991 and 1992 ones for N, but were higher than both
988 of them for P. That P was accumulating before masting is clearly demonstrated. The rise in P
989 at the end of the litter fall series, but not of N, in 1998 is also remarkable (Table 2). The 1998
990 litter was collected immediately before a masting like the 1992 one, so they could be
991 considered comparable in this respect even though the previous mast fruiting events were 1
992 (unusually) and 3 years prior respectively. Averaging where possible values in Table 2 for
993 2011 and 2002, and separately those for 1992 and 1998, gives composite estimates of leaf
994 concentration respectively immediately post and prior to masting: N: 16.73, 18.80 (+12.4%),
995 P: 0.615, 0.825 (+33.9%), K: 5.00, 2.44 (–51.1%), and Mg: 3.42, 2.53 (–26.0%). These inter-
996 mast changes suggest that N and P were depleted by fruiting and restored for the next event—
997 proportionally three-fold more for P than N, but the opposite occurred for K and Mg.

998 Reproductive allocation of N, P, Mg and Ca was in the order of 8 to 16% (Table 3),
999 but for K it was considerably higher at 37%. This last value can be traced back to the
1000 relatively high concentration of K in *M. bisulcata* pods, slightly higher than in leaves. The
1001 fruit to leaf mass ratio reached almost 0.6 for K compared with < 0.2 for the other elements.
1002 These calculations do not include root allocation, however, because estimates for them are
1003 lacking, in terms of both root growth rate per year and root concentrations. It would appear
1004 that fruiting in *M. bisulcata* is much costlier in terms of K than of P.

1005 **Table 3. Concentrations of the five macro-elements in fallen mature seeds and pods (= fruits) of *M. bisulcata*.** Collections were made during the 1998
1006 masting event, together with concentrations of the same in mature leaves of this species collected in the same year of a previous (1992) event. Prominent
1007 values are shown in boldface.

	Concentration (mg g^{-1})			Amount (kg ha^{-1} yr^{-1})[c]				Ratio	Reproductive
	Seed	Pod	Leaf[b]	Seed	Pod	Fruit	Leaf	[fruit: leaf]	allocation (%)[d]
N	14.5[a]	3.80[a]	22.3	0.770	3.728	4.498	41.924	0.107	9.69
P	1.80[a]	0.24[a]	1.18	0.096	0.235	0.331	2.218	0.149	12.99
K	7.40	6.13	5.91	0.393	6.014	6.407	11.111	**0.577**	**36.57**
Mg	3.01	1.17	3.77	0.160	1.148	1.308	7.088	0.185	15.58
Ca	3.77	2.17	13.2	0.200	2.129	2.329	24.816	0.094	8.58

1008

1009 [a] as reported in Table 1 of Green & Newbery [83]; [b] mature, green leaves, from Chuyong *et al*. [70]; [c] using estimates of oven-dry mass per ha from Table 1 of
1010 Green and Newbery [83]: seed, pods and fallen litter: 53.1, 981.1, 1880 (kg ha^{-1}) respectively; [d] RA = fruit density/(fruit + leaf densities).

Microberlinia bisulcata leaf litterfall rates in the 12-month July-to-June periods of 1990–1991 (non-masting in 1991) and 1991–92 (masting in 1992)—found by integrating the areas under curves of litter fall versus time in Fig 2d of Chuyong et al. [70]—were practically the same (1710 and 1670 kg ha^{-1} yr^{-1}, respectively). Multiplying these values by their corresponding P concentrations (Table 2), led to a difference of 0.168 kg P ha^{-1} yr^{-1}, which is very close to 50% of the investment in masting in 1998 (Table 3), assuming that the mast fruiting that year was similar in intensity to the one in 1992.

Discussion

Mast fruiting — a non-stationary process

If masting is driven by availability of resources, and these are partly stochastic and partly trending over time, then a range of interval lengths might be accommodated for *M. bisulcata*. In reality this range is limited to 1 to 3 years. The extended time series showed that between 1989 and 1995 there was a 3-year cycle, but after 1995, as radiation increased, there came a double year 1997-98 with high fruiting—1998 somewhat weaker than 1997, and then the cycle dropped to 2 years with a masting sequence 2000, 2002, and 2004, returning to very strong masting in 2007 and 2010 on a 3-year cycle, and finally after that the control seemingly weakened and resulted in two double-years, 2013-14 and 2016-17, which showed only moderate mast fruiting. Apart from being quite short at 29 years, the time series was non-stationary. There would be little reason to assume that it would a priori be stationary, especially, given the late transient cycle stage of the stand [63] and the varying climatic variables on all time scales ranging from years to decades and centuries [104, 105]. The inconstancy might be best understood in a novel way with a two- or three-factor threshold model, where C, P and K reach potentially different thresholds, simultaneously or

1035 sequentially. Thresholds themselves may not even be constant over time but relate to age,
1036 climate trends, and other tree-internal demands. When one of the resources reaches its
1037 threshold early, its effectiveness could be limited by the slower accumulation of another
1038 resource. The first resource will need to be stored or allocated elsewhere in the tree, even to
1039 then support the acquisition of the lagging resource. In time the second resource accumulates
1040 to a level that crosses a pre-set threshold, and this allows the first resource to come into
1041 operation.

1042 The allocations of C to mast fruiting in *M. bisulcata* are substantial. The earlier mast
1043 fruiting event of 1995, 28 out of 30 trees recorded had fruits. The average number of seeds
1044 per tree was ~26K (maximum 92K). Using estimates of mean dry masses of seeds and pods,
1045 and mean numbers of seeds per pod, the total dry mass investment was 17 and 307 kg per tree
1046 respectively, summing to 324 kg per tree [83]. These per-tree masses translate to 53 plus 981
1047 = 1034 kg/ha, ~55% the mass of average annual leaf-fall [83]. Applying the individual seed
1048 and pod masses to counts made for the 2007 and 2010 events, for trees that had pods [68],
1049 gave 181 kg per tree in 2007 and 122 kg per tree in 2010. (Excluding the two zero-producers,
1050 output values for 1995 were 346 kg/tree.) On this basis the investments per masting tree in
1051 2007 and 2010 were 52 and 35% respectively of that in 1995, illustrating an up to almost
1052 two-fold variation in masting intensity across these full fruiting events. Other more semi-
1053 quantitative scorings of mastings across the rest of the time series suggest a similar range in
1054 reproductive output.

1055 Flowering is a precondition to fruiting, but the dependence is not exact. Heavy
1056 flowering was recorded in 1992, a mast year; but in 1991 there was also especially heavy
1057 flowering but no mast fruiting [55, 103]. In 1990 there was some low fruiting (flowering
1058 unmonitored), this coming though in the year after a main mast fruiting in 1989: further, 1993
1059 had very little flowering and consequently almost no fruiting, and 1994 relatively high

flowering but only scattered individuals fruiting [78, 83]. From the later, more detailed, phenology recordings, 1995, 1997, 1998 and 2000 had strong flowering and were masting years, whilst 1996 and 1999 flowering was practically absent and had no masting [10]. Whilst valvate bracteoles protect flower buds before anthesis, it is possible that the intense occasional shower could damage flowers enough to interfere with pollination. This is the surmise for 1991, two years after the 1989 masting: fruiting was probably checked and masting was delayed to 1992. In 2004, the dry season started 43 days after 1 December 2003, on 12 January 2004 [10]: recall that the dry season for a given year starts in December the year prior. Flowering peaked over the week before and after that date. But in 2012, the season started 21 days in, on 22 December 2011, which was 1 month before flowering started in 2012, and ended another month later. (In both 2004 and 2012 there were no heavy showers that could have disturbed pollination in the first halves of those dry seasons.) These facets indicate that, firstly, occasional external and unpredictable influences can alter the processes behind a masting cycle; and secondly, the timing of flowering (also linked to the timing of leaf-exchange) can change by up to a month with respect to the start of the dry season. If internal tree nutrient levels do, via deterministic physiological mechanisms, trigger the flowering—which leads most often to fruiting at some level of strength [10], masting remains also subject to climatic stochasticity causing interference to pollination (may be once in 10–15 years) and variability in dry season timing and intensity (every year).

Abortion of small immature green pods falling to the ground was not seen in the 29-year period. It remains possible that outside of the three more intensively recorded periods this phenomenon was missed. If in occasional years there was strong flowering but no mast fruiting followed, then usually those trees that did develop any pods carried them through to maturity. The control of masting therefore most likely happens before flowering (see [10] for

further discussion). After that seed failure is simply a chance unpredictable cost within the evolved life history schedule.

Nutrient resources — interdependencies

Analysis of the seed and pod nutrient concentrations and amounts in relation to those in mature leaves indicated ratios of between ~ 0.1 and 0.2 for N, P, Mg and Ca, but substantially higher at 0.6 for K. This difference is very largely due to the low concentrations of the first four elements, and a much higher one for K in the pods. Pods were collected recently fallen. Caesalp pods are hard and rather water-repellent for several weeks, so it is very unlikely they adsorbed much K coming down in canopy throughfall (G. Neba, D. M. Newbery and G. B. Chuyong, in prep.), or were they leached to any extent. Had that been a cause of an increase, then Mg should have increased too, yet it did not. Presently it is difficult though to explain why so much K was being invested in pods. The comparative leaf K values, coming admittedly from a retranslocation study where replication of bulked samples per date was small, do closely match those of mature leaves of plantation-grown *M. bisulcata* trees (averaging ~ 5.8 mg $g^{-1;}$ at ages of 13 to 18 years; D. M. Newbery unpubl. data). Whilst ectomycorrhizas are strongly linked to P acquisition and uptake in the P-poor soils, K is also very low in availability at Korup [60], and the surface-soil root mat (with dense mycorrhizal networks) is an efficient collector of K (and Mg) coming down in throughfall (G. A. Neba, D. M. Newbery and G. B. Chuyong, unpubl. data). In plots at the same site, Chuyong [103] found N, P, K, Mg and Ca concentrations of 13.8, 2.09, 6.41, 2.22 and 3.50 mg g^{-1} respectively in *M. bisulcata* seeds that fell in 1992. Pods were not separated in the 1992 general collections but included within 'all reproductive parts' in the HEM plots, those with high abundance of *M. bisulcata* had a mean K concentration of 6.04 mg g^{-1}. Although other elements in fruits were albeit a little higher than for *M. bisulcata* alone in 1998, the earlier

1108 data confirm the K values of interest well. Investing P in seeds would presumably be
1109 important to the survival of establishing seedlings up until the time they could become
1110 infected with ectomycorrhizas and link into the mycelial network. Could it be that also K, not
1111 P alone—as for some time thought [61, 73], is a second key controlling element of masting in
1112 the Korup groves? Several indications suggest that P and K might act synergistically.

1113 The main pattern explaining the masting time series was the sequence of relatively
1114 wet dry season followed by relatively dry one. There was no evidence of water limitation to
1115 large trees in the dry seasons because of their ability to root deeply [67, 69], so this points to
1116 a soil or nutrient factor governed by soil moisture content in the upper soil layer, where fine
1117 roots and ectomycorrhizas form a root-mat and are most abundant and active in nutrient
1118 cycling. What is it about relative dryness and wetness of the dry months that leads to these
1119 relationships? Possibly dryness affected the fine roots and ectomycorrhizas. The drier the dry
1120 season, then likely the more restricted the root activity under limiting surface soil water
1121 conditions; which would possibly signal stored P in the ectomycorrhizas to be moved to
1122 intermediate locations ready for fruiting, and less would be used in maintaining new root
1123 growth. In a relatively wetter dry season this root activity would continue longer and more
1124 effectively, so that any additional P stored in the roots would stay there and not be signaled
1125 away to fruiting. Nevertheless, the main mineralization and uptake occurs in early weeks of
1126 the wet season [71], and this would be similar each year once the soil water content was high
1127 enough. This dryness is thought to be a proxy for a mechanism that triggers translocation, but
1128 it is one that cannot operate without the previous year acquiring more P, and setting up a form
1129 of 'relay'. It is interesting that moderate 'm' events occur in double-years and twice later,
1130 mirroring the two strong 'M' years 1997–1998.

1131 At Korup in the HEM plots, sand, silt and clay proportions were 77, 9 and 14%
1132 respectively [69]. There exist very few published water content vs water potential curves for

1133 sandy loam tropical soils, but at a site in NE Brazil with a very similar physical composition
1134 to Korup, Fisher et al. [106] found that a change in SMC (at 30 cm depth) from 20 to 12%
1135 (cf. the wet-to-dry-season change in Fig 3) led to a decrease in soil water potential (SMP)
1136 from –10 to –100 kPa—which is very much higher than the generally accepted value of –
1137 1500 kPa where wilting starts. Such a translation across sites should however be treated
1138 cautiously because any SMC-SMP relationship is finely dependent on the exact physical
1139 composition of the soil [107]. Wilting of understorey treelets and shrubs, even in the
1140 strongest dry seasons, was very rarely observed at Korup. Nevertheless, the drying of the top
1141 surface soil with the root mat might still be expected to affect nutrient uptake capabilities in
1142 the dry season. In those dry months the surface leaf litter is definitely dried out, and in many
1143 places the sandy-loam soil just below the organic layer is visible which leaves the root mat
1144 exposed. The implied sensitivity of fine roots and ectomycorrhizas of *M. bisulcata* to surface
1145 soil water conditions might in part result from this species very pronounced buttressing and
1146 an extensive lateral root system lying just below the surface soil mat [67].

1147 A cycle of 3 years would most likely allow a restocking of P, not only enabling
1148 growth of other tree parts, but also storage of P in wood rays and roots ready for fruiting (as
1149 the model later explains). A 4-year cycle could arise but, *ex hypothesis*, that would need a
1150 sequence of two dry dry-seasons: none was recorded however. The regression modelling
1151 gave an indication of year-to-year increases in radiation, and positive deviations from the
1152 smoothed trend of radiation with time. Changes were relatively small, radiation varied rather
1153 little from year to year, both for the dry seasons and the years as a whole. The additional
1154 radiation probably did not contribute to much increase in photosynthesis which would cater
1155 completely for the extra demand in years of masting, above the potential competition for C by
1156 leaves, stems and roots. Variation also in start and duration of the dry season, with the fairly
1157 steady daily radiation inputs, meant that there was probably sufficient radiation supplying C

1158 on top of tree storage, to meet the high dry mass investment in fruits. Carbon supply was
1159 therefore likely not the limiting factor to masting. One way to resolve this possible
1160 contradiction is to propose that, internal to the tree, there was strong temporal division in the
1161 allocation of C between rooting (one year, more wet) and fruiting (the next, more dry).
1162 Further, the lack of a relationship between proportion of crown fruiting and tree size may be
1163 further evidence that C is not the primary limiting factor for mast fruiting (contrary to what
1164 was originally suggested by [83]), if it can be assumed that large trees store more NSCs than
1165 small ones. The lack of year-to-year differences in oil palm yield relating to radiation is also
1166 moderate evidence of C from photosynthesis not being so critical for their yielding either.
1167 Palms can store up to ~20% of their C in stems from year to year [108, 109]. The lack of
1168 correspondence between oil palm yield and *M. bisulcata* fruiting suggests no common
1169 climatic driver and points indirectly to nutrients as the key factor in the forest, though
1170 possibly not P alone since palms did not respond to P fertilizer.

1171 The very few studies on C and nutrients involved in mast fruiting of dipterocarps that
1172 have been made largely support the thesis of this paper. Defoliation and girdling experiments
1173 on branches of *Dryobalanops aromatica* trees by Ichie et al. [110] indicated that flowering
1174 drew on C stored in local branches and the filling of fruits came from nearby leaves. This
1175 confirms the many similar conclusions for temperate trees mentioned in the *Introduction*.
1176 Relative allocation of P to fruits was shown to be higher than of C and N for of another
1177 masting dipterocarp, *Dipterocarpus tempehes* [9], again emphasizing the importance of P in
1178 reproduction, especially on P-poor tropical sites. During a different masting event for *D.*
1179 *aromatica*, Ichie and Nakagawa [111] found that P concentrations in branch, stem and roots
1180 steadily decreased during flowering and fruiting (but not in twigs and leaves), N fluctuated
1181 slightly (in all parts) and, whilst K decreased during flowering, it increased during fruiting (in
1182 all parts). Of the P needed for fruiting, 68% was estimated to come from branch storage,

compared with only 20% for N and very little for K. This was the first time root-stem-branch stored P was shown to be important for masting, and the result corroborated the hypotheses of Henkel et al. [8] and Newbery et al. [10]. A further study at the forest stand level provided more support for P and K both being key nutrients in mast fruiting. Aoyagi et al. [112] followed nutrient fluxes in soil, stems and fine litter in a lowland dipterocarp forest during one such event and for 4 years afterwards. Fluxes of P and K were much higher in total fine litter in the mast year than later years, whilst those of N, Ca and Mg altered little; the higher P and K was coming from the high allocations to fruits. Interestingly, P and K concentrations in coarse roots—but not stems—of the most abundant dipterocarp, *Shorea multiflora*, decreased more in flowering than non-flowering trees. This might indicate root storage of P and K ahead of stem and branch storage, in preparation for fruiting. Kitayama et al. [113] have more generally demonstrated in NE Borneo that across a P-use efficiency gradient, forest trees allocate proportionally much more P than C or N to reproduction (in relation to total allocation), even at P-poor sites.

Related considerations concerning carbon

The internal distribution of C between potentially competing sinks within each tree has a further interesting aspect. A majority of the *M. bisulcata* trees in the grove are presently of large to very large (≥ 50 cm stem diameter) sizes which means they likely have considerable respiration and maintenance costs. Carbon at least would not be so readily available in an average year to sustain such a heavy fruiting without causing deficits in growth elsewhere in the tree, perhaps in fine root and ectomycorrhizal production. This would lead, hypothetically, to an even stronger competition between rooting and fruiting, once stem growth is partitioned aside. That seedlings and saplings survive very poorly close

1206 to adults, led to the proposal of a reverse drain operating towards the old adults especially in
1207 mast fruiting years, for P as well as for C [55, 75, 76, 114].

1208 Previous estimates of leaf litterfall were 1880 and 1380 kg ha^{-1} yr^{-1} in non-masting
1209 1990 and masting 1989 respectively (the first estimate is used in Table 3), and came from
1210 Green and Newbery [83], who in turn based their calculations on January-to-December, plot-
1211 level, leaf litterfall estimates given in Newbery et al. [69]. The 1990–1992 data later indicated
1212 39% of that litter was from *M. bisulcata* trees. This 0.74:1 ratio may have been an
1213 overestimate, because it used calendar year estimates which would have missed linking
1214 November-December litterfall with that in January to April prior to masting, and the newer
1215 1990–1991 species-specific data were more precise. Or, it simply reflects variation in
1216 litterfall, viz. 1380, 1880, 1710 and 1670 kg/ha over the four years 1989 through 1992, which
1217 suggests that C supply was likely again not to have played an important role in determining
1218 mast fruiting since in around one masting event there was an implied cost to leafing and
1219 around the other none. The fruit-to-leaf amount ratios and reproductive allocations
1220 percentages in Table 3 may well be ~10% lower than the true values, if the 1990–1992
1221 litterfall estimates did apply. The 1990–1992 data also display a small shoulder in May 1992,
1222 possibly the result of the last older leaves being exchanged for the new green pods.

1223 Green pods stay on the trees for more than 5 months and therefore will contribute C to
1224 their structures and to developing seeds. This is likely an important source, and pods and
1225 seeds may indeed be almost autonomous in this respect. Pods are also held up high on the
1226 outer canopy edges where their photosynthesis is maximized [68]. Bennett et al. [115]
1227 reviewed the role of pods in their photosynthetic capacity, and Zhang et al. [116] provide a
1228 detail analysis of C balance in the pods of *Medicago sativa* to show the considerable C inputs
1229 that are possible. This source of C would make the *M. bisulcata* trees at masting even more

independent of C stores within the rest of the tree. It might explain the effect of raised radiation in the current fruiting year when compared with the one prior.

That stem increment growth was positively related to current year radiation but mast fruiting was not always, or at least not so strongly, suggests that C from photosynthesis was being used for stem growth and in mast years it was additionally contributing to mast fruiting. An internal trade-off between root growth plus ectomycorrhizal activity to enable the uptake of nutrients allowing nutrient uptake, and an allocation to fruits and seeds when cued, may probably well be the basis to the masting cycle. In the year following a masting, relatively more C would be allocated to roots because, if fruiting is 'switched off', roots become the main alternative sink; and then if in the second year there is sufficient P to cross the threshold, with some increase in radiation and extra C input, a next masting would occur after 2 years. If P accumulation was limited the tree would wait until the next year, forming a 3-year cycle. Extra C available in that second interval year might then determine the intensity of the masting ('M' or 'm'). A notable difference between P and K, is the rate of change in concentration in the leaf litter as the interval between mast fruitings progresses: P increased slowly over 3 years but K rose rapidly then fell lower than at the start. This might imply faster recycling of K than P, with a stronger withdrawal of K than P at senescence later as storage cells were being refilled prior to masting.

Rainfall and nutrient uptake

The important effect of mean daily rainfall in the dry season is dependent on the pattern of rainfall distribution over time, through the dry season and just into the early wet season weeks, that is up until the 100 mm threshold defining the season is exceeded. The first week's rainfall governs root growth and ectomycorrhizal physiology, and the later ones connect to the early wet season and the throughfall which primes the start period of optimal

leaf litter decomposition [71, 72]. A dry season may well limit root activity, and it also would delay decomposition: one which was short would only affect the former. On the other hand, a relative wet dry season will be expected to restrict rooting and ectomycorrhizal activity much less and encourage the earlier start of decomposition, both processes leading to better nutrient uptake into the trees. Ectomycorrhizal activity doubtless plays a role in P uptake, and the regrowth and maintenance of the root mat itself determines the level of retention of K leached from the canopy and its uptake.

An important aspect in connection with P-supply for fruiting, is how P is taken up and stored in inter-mast years. In the dry season of 1988–1989 and 1990–1991 there were pronounced peaks of P in fallen leaf litter in the HEM but not LEM plots [69]. This peak was absent in 1989–1990, directly after the heavy mast fruiting. The HEM litter would have been composed of ~80% *M. bisulcata* leaves [70]. In a relatively dry dry-season with likely more die back of fine roots and ectomycorrhizas than in a wetter one, P might be translocated out of these fine roots and ectomycorrhizas, going into storage for fruiting. Taken together the integrated aspects of this P nutrient cycle do provide reasonably strong support for P storage and use leading up to, and during, the masting events as proposed by the original PACER hypothesis.

Another result providing important evidence for P-storage is from the comparison between concentrations and amounts in the years across masting intervals which suggests further that the 50% of P used in masting was coming from retranslocation of P out of senescing leaves a few months before, probably stored in branches; and by difference it might be deduced that the other 50% was older and coming from local branch/wood storage built up in the prior 1 or 2 years, still within the interval. That result would fit with the notion of a temporary store for P and not all of the P needed for masting could be supplied in the current year alone. Rosell et al. [117] in a study of a range of tropical tree species found the inner

bark of branches was especially important for NSC storage and, although not yet tested, this may be where P is also held, ready for fruiting. Jones et al. [118] indicate this as a possibility for premontane tropical forests.

If P in leaf litter is relatively low in concentration after allocation to fruiting ([69], and new evidence in this paper), then the fast-forward cycling proposed by Chuyong et al. [70] could be temporarily slowed because mineralization by saprophytic fungi would have a low P litter resource to decompose. Root activity would either need to become more intense and efficient to take up the now lower soil levels, or at this time the ectomycorrhizal activity would come more to the fore by not only accessing low molecular-weight organic P molecules efficiently but also by effectively reaching low-concentration inorganic P sources further way from roots. This impasse would strongly select for the several co-adapted root mat and ectomycorrhizal traits seen in the field in order to achieve restocking of P. The rise in P accumulated just before masting could lead to higher P in litter falling that year which on one hand would mean fast re-uptake but on the other appears to be a dissipative risk when the perceived strategy is to save P (in the tree) for immediate use in fruiting. However, the ectomycorrhizas being part of the whole tree system, and cycling highly efficient, P is being 'saved dynamically' within the nutrient cycle. Also, N and K would in parallel complement C in stores — the latter benefitting from the small increase due to radiation enhanced photosynthesis, all three also needed for seeds and pods. That P was high in falling litter just prior to masting might furthermore indicate that P stores were quite full after a 2-year interval, and some of that 'extra' P was also coming from root retranslocation.

The analysis of mast fruiting in 1989–2004 [10] used 150 trees across the whole P-plot, but the later recording 2009–2014 used a subset of 61 trees in the eastern half, an area 100–500 N by 1000–1200 E, on the higher ground with denser stands and larger trees. The masting time series could potentially have been confounded by sampling extent changing

over time, because for the earlier half (1989–2004) it was found that masting was significantly stronger on the relatively higher and drier sites of this eastern part of the P-plot compared with the rest of the plot [10]. Allaying these doubts, the full and strong mastings in the second half (2007 and 2010) were confirmed by seed trapping across the entire plot [68]. The two double-years, in the second half of the time series, were only moderate mastings despite being at the more favorable topographic location.

The very strong mastings achieved by *Dicymbe corymbosa* in Guyana, with 3–4 t dry pod and seed mass per ha, were associated with pronounced El Nino Southern Oscillation (ENSO) peaks in radiation [8, 119]. However, this ectomycorrhizal detarioid, although phylogenetically very close to *M. bisulcata*, is unusual in that it reproduces annually also by sprouting, which must impose a considerable demand on C and nutrients for growth. For this reason, it might be conjectured that C stores are probably being continually used up and hence, to achieve a mast fruiting, a dependence on an additional boost of incoming radiation in those ENSO years would be necessary. Again, in contrast to most African detarioids (including *M. bisulcata*), *Gilbertiodendron dewevrei*—which forms monodominant stands in Central Africa—exhibits mast fruiting which is spatially unsynchronized and at irregular intervals [120]. Its individual seeds are very heavy (~30 g), so the mass allocated to reproduction per tree is probably far greater than for *M. bisulcata*. Compared with SE Asia and C. and northern S. America, the lack of a strong ENSO signal in C. Africa is pertinent [121, 122]. Masting in dipterocarps may well be for different suite of factors from those controlling the detarioids, achieving an evolutionary stable strategy along an alternative channel.

The interference effect of herbivores

The loss of a 2- or 3-year cycle in masting after 2011 suggests that the rhythm of wet/dry dry-season release of nutrients needed for full masting was disrupted by a combination of lack of an alternating pattern in rainfall plus heavy caterpillar attacks. This latter unforeseen intervention, combined with an unusual climate regularity over 3 years, acted as a 'quasi-treatment' in that C gain and storage were likely temporarily reduced. From the above argumentation it was not so much the decrease in C to supporting fruiting that was alone important but also the loss of C input for roots to allow P to be taken up and accumulated even in the relatively wet dry seasons. With some commitment to flowering already, leaf grazing would have nullified any C input from the local branches attacked to fruiting, requiring the tree to draw on stores in the branches. Nevertheless, some fruits resulted, indicating a means by which tolerance to herbivory could have occurred [102]. The caterpillar attacks may have interfered with the accumulation of P and thereby interrupted masting in full, leading to the unusual double 'm' years. The evidence of an herbivore effect is strongest for fruiting in 2013–2014 because of the detailed phenology data in 2011–2012. It is tempting to suggest that something similar might have been happening in 2015 before the very similar masting pattern of 2016–2017: alas, herbivore and tree phenology records were not possible during those later 3 years. A further unknown aspect is how herbivory may have induced stress hormones in the trees which, interacting perhaps with K levels, affected cytokinin concentrations.

The pooled field notes and observations suggest two lepidopteran herbivores occur in the crowns of co-dominant *M. bisulcata* and *T. korupensis* in the natural old-growth forest of Korup. Both species have pinnate leaves—*T. bifoliolata* does not—and similar stem density (~ 3.5 per ha for ≥ 50 cm DBH; [55]), but *M. bisulcata* trees are the greatest in size with a near-zero mortality rate over recent decades [63]. If caterpillars indeed fed only on expanding leaves (or flowers), then severe damage could ensue quickly, within 1 to 2 weeks, inducing

premature abscission (or lost pollination). For example, within 1 week caterpillars defoliated young leaves in crowns of two monodominant leguminous tree species in rain forests of Brazil and Gabon [123, 124]. Such phenomena are quite easy to miss though. This could explain why the black caterpillar was not noticed before at Korup, but it is unlikely the same reason for the yellow-caterpillar given the extensive multi-decadal phenological monitoring of *M. bisulcata* [10, 55, 102]. The detailed monitoring between 2009 and 2013, like that between 1995 and 2000, did not note any caterpillar attacks. To have an importance they would surely have been seen before from their feeding effects (droppings, noise of chewing, fallen individuals, hanging threads, frass in traps). Many other periods of intensive work back to 1984, focused in the dry months and early wet season when caterpillars would occur, did not record them. Whether these outbreaks are triggered by favourable climate factors, or palatable leaf chemistry or less parasitoid pressure, either perhaps induced by drier conditions [125] or simply mounting abundance over years [126], is unknown. Herbivore attacks to flowers, occurring stochastically, might be viewed as being similar in end effect to intense rainfall events disrupting pollination: both limit reproduction.

Refined updated hypothesis for mast fruiting in caesalps

The mast fruiting cycle in *M. bisulcata* might be explained in terms of the availability of three principal resources which control the timing of reproductive output: the limiting resource P, a controlling resource water, and qualifying resource C. If sufficient P accumulates within 2 years to trigger flowering and there is sufficient C coming from storage laid down over the last year or supplemented due to a positive radiation difference between prior to current year, then fruiting is to be expected. But when P is slower at accumulating, the interval is extended by one year and fruiting happens within 3 years. It is highly likely that in the latter case C would still be sufficient either from reserves laid down in the tree in

the previous year and/or a small surplus the current year of fruiting. When there is sufficient P accumulated after one year but not quite enough C for a full masting, fruiting may follow anyway at a moderate level; and in doing so it is likely that not all of the accumulated P would have been allocated 'as planned', and the part remaining, plus last year's continuing uptake, will sustain a second moderate fruiting. On grounds of resource requirements, it is difficult to see how the pattern could be 'm-M' or 'M-m', and neither of these were observed: in the first, there would be insufficient time after a 'm' fruiting to build up P so rapidly to have an 'M' one, and in the second, the 'M' first would exhaust P levels down below a threshold and no 'm' would likely be possible either. The pattern M-M did occur once, however, at the time of an exceptional rise in radiation levels over a 3–4-year period: it can only be hypothesized that there was unusually even more surplus C for extra root growth and P uptake in both the year preceding the first 'M' year and during the second one. The main processes leading to mast fruiting in *M. bisulcata* are schematically summarised in Fig 5.

Fig 5. A schematic flow diagram of the interrelated hypothetical processes behind mast fruiting (M) in the grove-forming population of *Microberlinia bisulcata* at Korup. The boxes with light blue shading are either empirically established in the present study, or at least can be strongly inferred from the literature. They involve the deterministic factors soil phosphorus (P) and potassium (K), and the stochastic effects of dry-season (DS) rainfall; SMC means soil moisture content, and ECM stands for ectomycorrhizal. Those in grey concern radiation and carbon (C)-supply, dynamics and allocation. The box in pale brown-orange concerns the likely important role of ectomycorrhizal networks and nutrient fluxes within the root mat, which are hypothetical and require empirical confirmation. The central double-headed arrow represents the interplay between within-tree and between-tree processes. Green shading and lines indicate the proposed threshold triggering flowering and fruiting, and repeated annual uptake and storage over successive years within the masting

cycle of typically 2-3 years. Hormonal control of masting, shown in yellow, is strongly suspected: it also requires critical testing. The small polygon in lilac, centre-left, is the primary condition for mast fruiting to occur, as shown by statistical model fitting in this paper (t is time in years). It is the process-link between the start and end of the diagram. Changes in the degree with which flowering results in fruiting, and in the intensity of fruiting itself (e.g. when lowered to 'm'), are explained in the main text.

An interesting aspect is the feedback control that might operate by way of C going either into fine roots and ectomycorrhizas, which would enhance nutrient uptake, or into wood storage (stem, branch and large root), which could sustain a next fruiting. The 2- or 3-year cycle is simply a consequence of the contingent conditions of these trees growing in low P soils aided by ectomycorrhizas. Rainfall and radiation are stochastic processes, to some extent inversely related, which overlies the intrinsic deterministic cycle: the important difference between them is that rain, acting primarily on the soil, facilitates P release, acquisition and uptake (needed to accumulate P), and whilst C is needed also for fruiting, it is essential for root production and maintenance of ectomycorrhizas that makes this P uptake possible. That root growth should always precedes fruiting in a masting year, the first in late-dry into early wet season (March–April), the latter in late wet season (September–October) decides the sequence unambiguously: C in the dry season will go to the root sink first and what remains stored, used for stem growth or reserved for fruiting when it happens. The low P supply is therefore the main determinant: C must be sufficient but does not appear to be decisive for the interval length. N and K will also be involved but the evidence more strongly supports the P thesis. Nitrogen is not limiting at Korup with ample N-fixation and aerial input [69], and whilst K follows P in being intrinsically quite low in supply in Korup soils, the root-mat appears to be highly adapted to catching and retaining canopy-leached K and so

enabling its efficient recycling (G. A. Neba, D. M. Newbery and G. B. Chuyong, unpubl. data). The K allocated to pods could, like N, be accommodated by wood ray storage.

Carbon and N will be important for masting, even when P and K are limiting and are the key storage resources, because all elements will be needed in their stoichiometric ratios in order to fill pods with seeds. As in other plant physiological problems, simplified reductionist approaches do not recognize the integrated nature of growth and reproduction. Carbon (sugars) and K are required for transport and storage, P will be bound into C-H-O structures which act as 'carriers'. It is possible though that a small increase in C from radiation might have a non-linearly disproportional benefit to P transport and storage. Understanding masting physiology requires an integrated and dynamic approach, one of shifting sink strengths over time. After a last masting, roots would likely act as the strongest sink, then the stems (and rays and bark) and branches—part growth, part storage, and finally reproductive parts. No abrupt switches in C, in contrast to a threshold switch for P, but a gradual altering of the components over a 2–3-year cycle occurs. For this to operate it is necessary to hypothesize a feedback from the C-depleted branches to the more C-depleted roots. With the fruiting sink removed, C should move from stems to roots. Whether this needs additional hormonal control is an interesting question. It remains a conundrum why 'in the background' to the rooting-fruiting axis, stem wood growth is positively correlated in a quasi-independent way with radiation. Stems may be working perhaps as the storage stabilizers, being placed centrally between shoots and roots. As they grow they store and balance the terminal demands. The levelling adjustment of C between the first and second interval years could perhaps explain the lack of clear correlation between fruiting (and inversely rooting) with stem growth increment. The time sequence within the year is also important here. In the second (drier) year of fruiting, C is not, *ex hypothesis* predominantly going to roots in the

1450 early wet season but more to stems for storage, and en route there for filling fruits later in the
1451 wet season (Fig 5).

1452 If radiation were to increase during an increasing part of a cycle or as a longer-term
1453 trend, and C were alone the limiting resource for masting, then fruitings would come closer
1454 together and this would defeat the putative economy-of-scale selection. In this respect a non-
1455 stationary time series offer advantages when matched to an also non-constant climate
1456 environment. On this basis it would seem also unlikely that C could be the key resource for
1457 *M. bisulcata*. Further, C available per tree will decrease with tree age after the point of
1458 maximum crown extension because of the higher respiratory loads incurred in maintenance of
1459 the whole tree. This may be connected with the observed crown thinning of the largest trees
1460 (J. M. Norghauer, unpubl. data). When seed production was substantial, in proportion to the
1461 high flowering per crown then there would be a deficit of C to fill pods, or pod production
1462 would decrease, or another cost incurred (e.g. at the roots or wood production). But the
1463 evidence was that in *M. bisulcata* the relative crown-cover with pods remained constant with
1464 size and, by broad inference, age. As a tree grew to have a larger root system with
1465 ectomycorrhizas to maintain, to acquire P and retain K, when absolute pod and seed output
1466 rose then the demand for P and K would have also. As with C and N, we can expect that P
1467 and K is stored in 'quick-release' forms in wood rays and bark of the stem and the main
1468 branches. A phenomenon often remarked is of one part of a large crown flowering and
1469 fruiting much more than the others, which could be explained by a correspondingly more
1470 active root system of the tree, and a matching storage of nutrients in the wood and branches,
1471 on that side. (See [67] for the strong crown asymmetry in *M. bisulcata*.)

1472 The arguments going from nutrient concentrations in fallen litter through to the
1473 possibly the trees building up and storing P and K before masting are tenuous because of the
1474 many uncertainties about the processes involved. If some translocation occurs out of leaves

before they are shed, then why are the P levels so high just before masting? If P was being actively stored for fruiting, it might be expected that it would be lower in concentration in the fallen leaves. However, the high concentration reflects that all the trees were well stocked with P by that time, the stores were full, or even over-full, and there was still plenty of P to fall. From earlier work, it was established that ectomycorrhizal species, especially *M. bisulcata*, drop P-richer leaf litter than non-ectomycorrhizal ones [69] partly because the retranslocation was less [70], and it was argued then that this allows the decomposition process to operate without P limitation, the 'fast forward' strategy. However, the concentration of K (to a lesser extent that of Mg also) reached a peak mid-interval and then fell just before masting. This could mean that K was being translocated into storage before fruiting. In general, the export of K and Mg from leaves of trees is usually low compared with that of N and P. Understanding the differences in dynamics of P and K in this context is highly challenging, and also explains why N showed no clear mast-interval trends. Whilst K was likely building up on soil colloids in wetter dry seasons, mineralized from fallen leaves, dead roots and old pods during decomposition, and this process was more limited in the drier dry seasons, suggest that K must also have been transported and actively stored in the tree between the prior and mast years. To recycle more K via litterfall would involve a potentially high loss due to leaching when the cation exchange capacity of the soil has already been reached, compared with the seemingly tighter and ‘safer’ direct access by ectomycorrhizas to organic P. This reliability aspect might then favour P over K as the better controlling factor in masting (Fig 5).

Phosphorus storage and control

What could the likely form of storage of P in trees be? Since Bieleski [127] the most likely candidate is inositol hexa*kis* phosphate (= phytic acid; $C_6H_{18}O_{24}P_6$). It has been shown

1499 many times to be the main storage form in seeds, and has been detected in stem and roots. It
1500 forms salts with Ca, K, Mg, Mn and Zn, and in soils occurs commonly bound to Fe. It occurs
1501 in 19 hexa-structures which are interconvertible [128]. It is viewed as the most frequent P-
1502 storage form when P is in excess, that is in passive storage; the P is readily retrievable and
1503 mobilizable. Other molecules can have seven or eight atoms of P but seem less common
1504 [128]. Inositol hexa*kis* phosphate is involved in cell metabolism, in ATP regeneration, RNA
1505 export and the repair of DNA. It is prominent in cell storage biochemistry, which may make
1506 it a candidate for *active* storage. However, so very little has been researched in this area, and
1507 accounts for trees are very sparse. A notable exception is the study of Kurita et al. [129],
1508 showing P storage in *Populus alba*, followed by release in spring, and indicating perhaps a
1509 common function in many deciduous tree species. It is conceivable that the same mechanism
1510 could operate in seasonal tropical trees and even be a basis to P storage for mast fruiting
1511 species. How inositol hexa*kis* phosphate is linked to polyphosphate formation in roots and
1512 mycorrhizas and comes under hormonal control remains unclear.

1513 In an experiment with *Eucalyptus grandis* seedlings, comparing low and high P
1514 media, Mulligan [130] detected stored P in the form of esters and residual P (mostly
1515 phosphorus proteins), especially in roots, and more so the low P medium. The idea is that
1516 these stores buffer the plant (maybe actively stored), from there P can be mobilized and sent
1517 to other stores in the shoots. In a similar vein, Netzer et al. [131] comparing mature *Fagus*
1518 *sylvatica* stands, one on high and one on very-low P available soils, found that in the latter P
1519 built up in roots in late summer, and from there was moved on to stem and branches,
1520 suggestive of at least two storage sites in a series enabling adaptation to the poor site.
1521 However, hardly anything is known about how P stores are internally controlled, or how
1522 hormones signal transfers of P [132], which could give even a lead as how P might be built

1523 up in stores in masting intervals, and once a threshold level is met how the switch to
1524 flowering is signaled.

1525 Much evidence suggests that senescence in leaves, and possibly pod formation, may
1526 also involve cytokinins ([133]. Chiou and Lin [134] have proposed different hypothetical
1527 models for inorganic P being regulated by cytokinins and sugar levels. How these promising
1528 models can be extended to storage and release of P has yet to be worked out. The strongest
1529 candidate for the elusive 'florigen' is now widely held to be a flowering locus T [FT-]
1530 protein, which again appears to be controlled by a cytokinin [135]. Cytokinins act at long
1531 distances throughout the plant and are bidirectional in their effects, both of which might
1532 hypothetically implicate them in inositol hexa*kis* phosphate metabolism and P storage. It
1533 remains likely that floral initiation in *M. bisulcata* takes place at the end of the wet season,
1534 before leaf exchange occurs in the dry season (see discussion in [10]). Earlier results on
1535 cultivated apple (*Malus*) trees suggested already that a two-way process of hormonal control
1536 could be operating [44], and the idea that sugars and other NSCs destined for the usually
1537 stronger root sink ([136] for mandarin (*Citrus*), [137] for prune (*Prunus*)—on K-deficient
1538 soils) might be diverted to the flowering meristem sinks under the control of gibberellins
1539 [138]. How exactly the 'switch' occurs remains elusive [45], and still to today. The precise
1540 consistency of alternate bearing in pistachio (*Pistacea vera*) orchards has been questioned on
1541 statistical grounds though [139].

1542 Active storage hypothesis

1543 Storage of C as reserves in trees (stem rays, bark and branch wood) was widely seen
1544 in the past as being passive. The C was being made available for regular annual growth
1545 processes in ways that optimized the economy of the tree [140]. Extending this idea to
1546 nutrients, Chapin et al. [141] produced a systematic table for N and P, reserves of the latter

mainly featuring as inorganic phosphate, polyphosphates, or phospholipids, leading them to conclude that dependence on mineral nutrients is likely much more pronounced than it is on C for reproduction. Sala et al. [142] argued that the build-up of NSCs in stores in trees might be acting as a buffer against stochastic variation in C inputs due to environmental stresses (e.g. drought, herbivore attacks), which as a bet-hedging strategy would insure against temporary collapses in maintenance and growth. The storage would need to be active, rather than passive, otherwise in the latter case it would be used up immediately in extra current growth. Extending this idea to mineral nutrients, Dietze et al. [143] hypothesized that N, P and K might also be accumulated and stored to guard against periods of reduced nutrient uptake, stabilizing the internal nutrient cycles. Hormones might therefore control source-sink processes actively. The empirical evidence for active vs. passive control of C storage in trees still remains weak and unresolved though [144]. But where P and K especially are limiting growth, evolution of such an active mechanism could be of considerable evolutionary advantage. Mast fruiting imposes a quasi-unpredictable (partially stochastic) demand on mineral nutrients supplies, and therefore for P and K active storage would serve it well, particularly in sites where uptake patterns themselves are subject to environmental stochasticity (the intensity of the dry season at Korup, for example).

Nutrients in alternate bearing of tree crops

Studies of alternate-bearing pistachio trees have provided several valuable insights into how tree nutrient balance changes between ‘on’ and ‘off’ years. Whilst fruiting depresses root growth in fruiting years, uptake rates from the soil remained similar. If N, P and K moved from uptake mainly to leaves and shoots in ‘off’ years, and to fruits in ‘on’ ones at 3–6-fold the investment compared with ‘off’-year uptake, this implies that stores were being drawn upon [47]. Trees stored 7- and 14-fold more N and P respectively in ‘off’ than ‘on’

years, mostly in branches, which also suggests active storage [48]. Of what went into fruits in an 'on' year, 70% of N and P came from storage, and 30% from retranslocation. For N and P, storage forms are well known (e.g. phosphoproteins), but for K they are not. K would need to be intensively taken up in the 'on' years (study cited here was made on well-fertilized plots, however), despite the slower root growth, transported and used immediately in the fruits [145]. Interestingly, K concentrations in pistachio are inversely related to NSC concentrations, because K is needed for sugar transport to the apices where fruits are being formed [133]. If this last process applied to *M. bisulcata* at Korup, K would be taken up in the mast years and, assuming also it cannot be stored in roots or branches, the only other feasible (temporary) store would be outside the plant, this is as exchangeable forms held on soil colloids, built up in the wetter non-masting years (G. A. Neba, D. M. Newbery and G. B. Chuyong, unpubl. data). How far K might be transported laterally in the mat by mass flow is unknown.

Picchioni et al. [146] further showed, for pistachio again, that N and P were translocated out of the mature pericarp into the seeds of the same fruits, although K was not, which left the pericarp relative rich in K on fruit fall (harvesting). This could have been happening in *M. bisulcata*, and in this way explains the K-rich pods. Possibly as pods browned they too moved N and P to the seeds. K having achieved its role in aiding sugar transport (under the hypothetical hormonal control suggested) would then be redundant as regards reproductive investment *per se*: the fallen pods would be leached much later by the end wet season rains, even some remaining until next year, and in this way returning the extra K to the forest floor and soil colloid sites. Returning to the question of possible CHO storage in 'off' years, direct estimates showed that very little of the stores laid down in those 'off' years (8%) contributed to the 'on'-year yield [147]—confirming again the general finding mentioned above in the *Introduction*. Overall, the main evidence is in favour of nutrients plus

hormones being the controllers of alternate bearing and, in extension, masting in forest tree species where nutrients are limiting.

Soil nutrient status

Nitrogen supply has been shown to be important for fruiting in *Nothofagus* ([148]. In either N-fertilized stands, or unfertilized ones when rainfall was high (allowing higher N mineralization), masting was enhanced, subject to a temperature cue also operating. Likewise, Leeper et al. [149] showed in N-poor sites, that masting of spruce was less frequent and less intense than at N-rich sites. Cone production was positively correlated with soil N in the year prior, not the current one. Both studies found lagged N-effects, implying that N was being stored. Nevertheless, unravelling the causes is difficult because the better, wetter, conditions one year for N supply are not conducive to floral initiation, which depends more on warm drier ones affording higher sugar transport to apices. An inherent inverse correlation often exists which leads to an unstable alternation: a similar pattern is proposed for *M. bisulcata* at Korup with the relatively wetter and drier dry seasons.

Evidence for depletion of nutrients during masting, needing then a restocking for the next event, is unfortunately limited. For white-bark pines, Sala et al. [150] showed that P and N declined in branches after masting—cones having especially high P concentrations; and this could be linked to the species being ectomycorrhizal. Depletion spread over other plant stores according to the amount needed for masting. Not only do Sala et al. [150] provide evidence of resource switching (from storage to reproduction), but weather seems to be cuing for masting by synchronized nutrient uptake being made possible. This supports the PACER hypothesis and the main thesis of the current paper on *M. bisulcata*.

Climate factors which affect nutrient resource availability driving masting was a central argument of the review of Allen et al. [42]. This underlying process is how economies

1620 of scale become operational: the predisposition of trees to avoid seed predation or increasing
1621 their flowering efficacy is enhanced by synchronization. Allen et al. [42] made strong
1622 recognition of the role of ectomycorrhizas, building on Henkel et al. [8] and Newbery et al.
1623 [10]. That either N or P (rarely both) are often limiting where ectomycorrhizas tree species
1624 are successfully dominant in forests, must place a high demand on these elements for seed
1625 production. A set of resource acquisition and storage traits that would benefit growth and
1626 defense in these nutrient-poor habitats generally would be expected to be channel-selected
1627 through evolution to support an optimal life history strategy [42]. Different storage routes
1628 could be postulated to work in temperate vs. tropical systems where respectively N and P are
1629 the more limiting. The Korup work posits that resource synchronization might, in part, be
1630 achieved via a shared mycorrhizal network. It is a working hypothesis that requires testing in
1631 the field at Korup. Given the lack of support for C storage being important for mast fruiting,
1632 clearly the C budget model of Isagi et al. [18] needs to be rethought in terms P uptake,
1633 storage and usage.

1634 Fernandez-Martinez et al. [14] recognized that many mast fruiting species grow in N-
1635 or P-poor soils, or at least on sites where the demand for these elements is high. The authors
1636 relied on foliar N and P concentration data. There are two problems with this approach:
1637 firstly, from among the masting species some samples may be from mast years, others from
1638 inter-mast ones pulling the differences between masting and non-masting species apart; and
1639 secondly, many species well adapted physiologically to nutrient poor soils do have nutrient
1640 levels similar to those on richer soils, but display different nutrient dynamics. Again, the
1641 obvious association with, and role of, ectomycorrhizas was overlooked. Contrary to the claim
1642 of Kelly [16], nutrients can be hypothesized to determine masting when their availability
1643 fluctuates, and tree nutrient concentrations are synchronized via the mycorrhizal network.
1644 Stronger competition between masting and non-masting neighbours need not be invoked (as

1645 proposed by [15]: it follows from ecophysiological adaption of the masting species to their
1646 nutrient-poor conditions. From the nutrient-supply model the other economy of scale factors
1647 can operate; in the case of *M. bisulcata* this would probably be mainly to satiate seed
1648 predators [151].

1649 Janzen [152] asked why the intervals between mast fruitings in dipterocarps are so
1650 large and irregular. That would not fit with resources like P accumulating to given common
1651 levels. Resources could doubtless be stored like NSCs, but not stored only for fruiting, and
1652 when not so used would be moved to other sinks such as roots. Dipterocarps form diverse
1653 mixtures of species in many forests, with their individuals spaced out among those of other
1654 ectomycorrhizal and non-ectomycorrhizal species. Thus the functioning of a shared below-
1655 ground network seems less feasible, especially when the fungal species differ across tree
1656 species. However, Janzen [152] interestingly raised the idea that masting may have originated
1657 in species when they were much more clumped in the evolutionary past than they are today,
1658 growing as patches of near single-species dominating stands. If nutrient resources were more
1659 commonly distributed, shared and equilibrated within such patches in the manner postulated
1660 for extant *M. bisulcata*, and over time the tendency to clump by some species degenerated as
1661 they locally formed mixtures with other tree species, then the nutrient-threshold mechanism
1662 behind masting may have lost its effectiveness.

1663 Tree-tree root connections

1664 Root grafts could potentially provide another means of nutrient transfer between *M.*
1665 *bisulcata* trees within groves. Soil surface grafts have been observed at Korup although as yet
1666 none anatomically investigated and mapped. Early field experiments on *Pinus strobilus* in
1667 North America by Bormann [153] point to this as a real possibility. It was suggested that the
1668 process would mostly operate between large dominant trees of similar size to enable an

1669 equilibration of resources across trees. Many temperate and tropical tree species form root
1670 grafts [154, 155], often close to stems and among large roots, but there is also evidence for
1671 grafts between roots at greater distances when the species has long surface roots, e.g. for
1672 *Dacryodes excelsa* (Burseraceae) in Puerto Rica [156], or among smaller roots well below the
1673 surface, e.g. in oaks [157]. The extensively spreading root systems of *M. bisulcata*, connected
1674 to large buttresses [67], make the crossing of roots at 15–20 m away from stems quite
1675 feasible. Because grafts form as a result of physical pressing together of roots, the restricted
1676 vertical space of the root mat would likely also encourage grafts between medium to small
1677 roots, and in this way create a large multi-nodal root network. Apart from possibly providing
1678 increased resistance to wind throw—which would not be important for *M. bisulcata* given its
1679 strong buttressing, and temporarily supporting suppressed, damaged or dying neighbours,
1680 other advantages of root grafts have not been so obvious [158]. However, synchronizing
1681 nutrient supplies between, and storage within, trees across whole clusters would clearly be
1682 beneficial and strengthen masting. Root grafts would moreover provide a strong 'platform'
1683 for the ectomycorrhizal network and faster local transfers. A role for root grafts enabling
1684 masting has recently been suggested by Noble et al. [159] to partly explain alternate bearing
1685 in pistachio in a year when pollination synchrony (the Moran effect) was relatively weak. The
1686 focus in this plantation study was on C as the putative resource being transferred.

1687 More directly relevant to *M. bisulcata* was the work of Yli-Vakkuri (1953), cited by
1688 Bormann [153], showing that P was moving across root grafts of *Pinus sylvestris*: the author
1689 made no connection to ectomycorrhizal status of pines or association of ectomycorrhizas with
1690 mast fruiting (see [52]). Conceivably, ectomycorrhizal and grafted root-networks might
1691 operate together within *M. bisulcata* tree clusters, either contemporaneously or in successive
1692 phases around the end of the dry into the early wet season. If hormones are also transportable
1693 across grafts, an added level of synchronizing control is afforded. The role of tree root

interconnections (ectomycorrhizas and grafts) becomes an essential auxiliary to the main masting hypothesis. Bormann [153] advanced the thesis that root grafts were established first by alignment of xylem tissues which rerouted water flow, and connecting phloem tissues permitted organic and nutrient transfer later. Between the mid- and late-ontogeny stages, *M. bisulcata* trees growing in dense patches become large adults, as described by the transient dominance model [63], and root grafting may have started when water was at a premium in the dry season. It then changed to having a more organic-flux transfer role once deep roots had secured all-year-round water supplies, the root mat had fully formed, the litter nutrient cycle was stable, and P (and possibly K) were by then in greater demand for growth and reproduction. To know whether or not codominants *Tetraberlinia bifoliolata* and *T. korupensis* graft below ground onto *M. bisulcata* would be interesting. That the three species do not usually mast synchronously suggests, though, that they probably do not form interspecific connections as predicted by Graham and Bormann [155].

Role of environmental stochasticity

Dynamics simulation models involving storage and thresholds, resource-switching in a randomly varying environment, yet with no economy of scale operating, are able to generate masting cycles when either the variation is strong (i.e. very good vs poor years occur) or, when the variation is not so strong, there is an increasing non-linear response to the positive variations [57]. Even then masting can be diluted over successive years and is not quite bimodal. Under weaker variation in the environment an economy of scale is needed to achieve a well-defined masting cycle [56, 160]. Such large differences between very good and poor years in terms of resources (assuming linear responses) are ecologically rather unrealistic though for medium-length time series covering fairly regular 2- or 3-year masting cycles. This in turn suggests that without an economy of scale a non-linear response is more

likely to be involved. An essential requirement of such masting would be to avoid degeneration of the time series into chaos—as shown by the models of Rees et al. [161].

The systems view would postulate a feedback control to avoid such chaos but it could allow for an unpredictable mix of 1-, 2- and 3-year cycles over time to the same effect in thwarting predator tracking. For a limited resource like P, such a system means regulation of internal fluctuations across the tree parts within a masting cycle, so that some equilibrium in the P dynamics is maintained medium-term. An economy of scale which itself involves a mechanism for P distribution would facilitate masting when based on storage and thresholds of that same resource. In this respect, ectomycorrhizal networks, which enable P acquisition and uptake (and possibly P storage), could bring about an equilibration of P across the connected roots of neighbouring trees, which would allow a contemporaneous storing and triggering of mast fruiting, as P levels rose in concert across all trees in the population (Fig 5). In the case of *M. bisulcata* in this study, the key climate variables vary in a somewhat normal way, and it is unlikely they can cue masting in a simple directly-linear manner. However, if wetter dry seasons lead to non-linear increases, or pulses, of P-and/or K-uptake, coordinated across the forest, synchrony is also possible. The network idea would also explain why one or both *Tetraberlinia* species often mast fruit along with *M. bisulcata*, because they largely share the same mycorrhizal species [61, 74]. The non-stationary aspect of the main hypothesis suggests a finely-tuned evolved ecophysiological system in *M. bisulcata* allowing it to respond to variation of the climate in order to maximize its fitness.

Conclusions

The results in this paper confirm and extend the findings based on those for 1989–2004 presented in the Newbery et al. [10] with greater statistical detail and confidence. It

1742 would have been valuable to know whether the 3-year cycle returned after 2017. Post-
1743 dispersal predation is currently important, especially in well-lighted gaps although not in the
1744 shaded understorey or below *M. bisulcata* crowns. It could have been much more common in
1745 the past when either *M. bisulcata* individuals were scattered across the landscape [62], or
1746 when grove dynamics was at the rebuilding stage [63]. Since, seeds and seedlings need P to
1747 establish and reach to the network of ectomycorrhizas, it would be evolutionarily
1748 advantageous for an ectomycorrhizal species to mast fruit and increase its chances of
1749 establishment. It is interesting that masting is achieved in the most clustered caesalps, and
1750 was not apparent for the more spatially dispersed species in southern Korup.

1751 Most of the C dynamics models for trees to date (e.g.[162-165]) do not cater
1752 adequately, if at all, for environmental stochasticity or non-constant reproductive allocation
1753 schedules. Source-sink models for herbaceous plants, let alone for more complicated trees,
1754 have made little conceptual progress in the last three decades since Farrar [166], Kozlowski
1755 [167, 168], Minchin and Thorpe [169], and Wardlaw [170], apart from raising an unresolved
1756 debate over passive versus active storage. They usually assume steady-state equilibrium
1757 conditions, are often teleonomic (e.g. [171]), and are strongly focussed on stem diameter
1758 growth and maximizing tree yield. They are, therefore, still too far away from an
1759 understanding of trees in natural forest ecosystems (see [172]) to explain even reproductive
1760 schedules like masting. Source-sink relationships, within trees especially, turns out to be very
1761 complicated: a more integrated systems approach is probably required. An important
1762 challenge is working out how P, K and N interact with C dynamics over the complete life-
1763 history schedule of a tree. A very interesting hypothesis coming from this extended
1764 phenological analysis is that both K and P levels might synergistically control mast fruiting of
1765 *M. bisulcata*, mediated by the physical structure and functioning of the surface root mat for
1766 nutrient cycling. To test this hypothesis further requires much more detailed recording of

nutrient processes at the tree-level and within the system, replicated over several mast fruiting events.

The literature review of the likely mechanisms lying behind mast fruiting in *M. bisulcata* gives valuable pointers to detailed aspects that need investigation. The most critical data for the nutrient resource limitation hypothesis would be phosphorus concentrations in roots, branches, leaves and fruits of a large sample of trees over several masting cycles. Detection of phytic acid in branch wood, prior to fruiting especially, could confirm that P was being stored. Lack of predicted changes in P over time would falsify the hypothesis. In addition, to test the related economy-of-scale mechanism for equilibration of P between adult trees at masting would require showing everywhere a flux of P through the mycelia of the shared ectomycorrhizal network, i.e. between neighbouring large trees.

The fundamental driving variable behind the deterministic mechanically-intricate system operating to cause mast fruiting in *M. bisulcata*, is the stochastic variation in rainfall (Fig 5). The vicissitudes of rainfall in the dry season over successive years could generate the non-linear differences needed to enable the storage process. Stochasticity becomes the ultimate 'causal' factor over evolutionary time. This can operate at Korup because P as a resource is strongly limiting the system, there is seasonality, and rainfall alters access, availability and uptake of P. The hypothesis argues for a fruiting-rooting trade-off as the basis to alternate bearing and masting. For a common nutrient threshold to operate trees must be spatially close and connected via their roots and mycorrhizas. The new evidence and analyses here, showing both climate and ectomycorrhizas can operate respectively on and within the forest nutrient cycle, makes a major step forward in refining the original PACER hypothesis [69].

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Supporting information

S1 Appendix. Radiometry at Bulu, Ndian: calibration and interpretation.

S2 Appendix. Evidence table for the levels of mast fruiting per year.

S3 Appendix. Time series analysis of dry season climate variables.

S4 Appendix. Regression model fits of masting on rainfall and radiation.

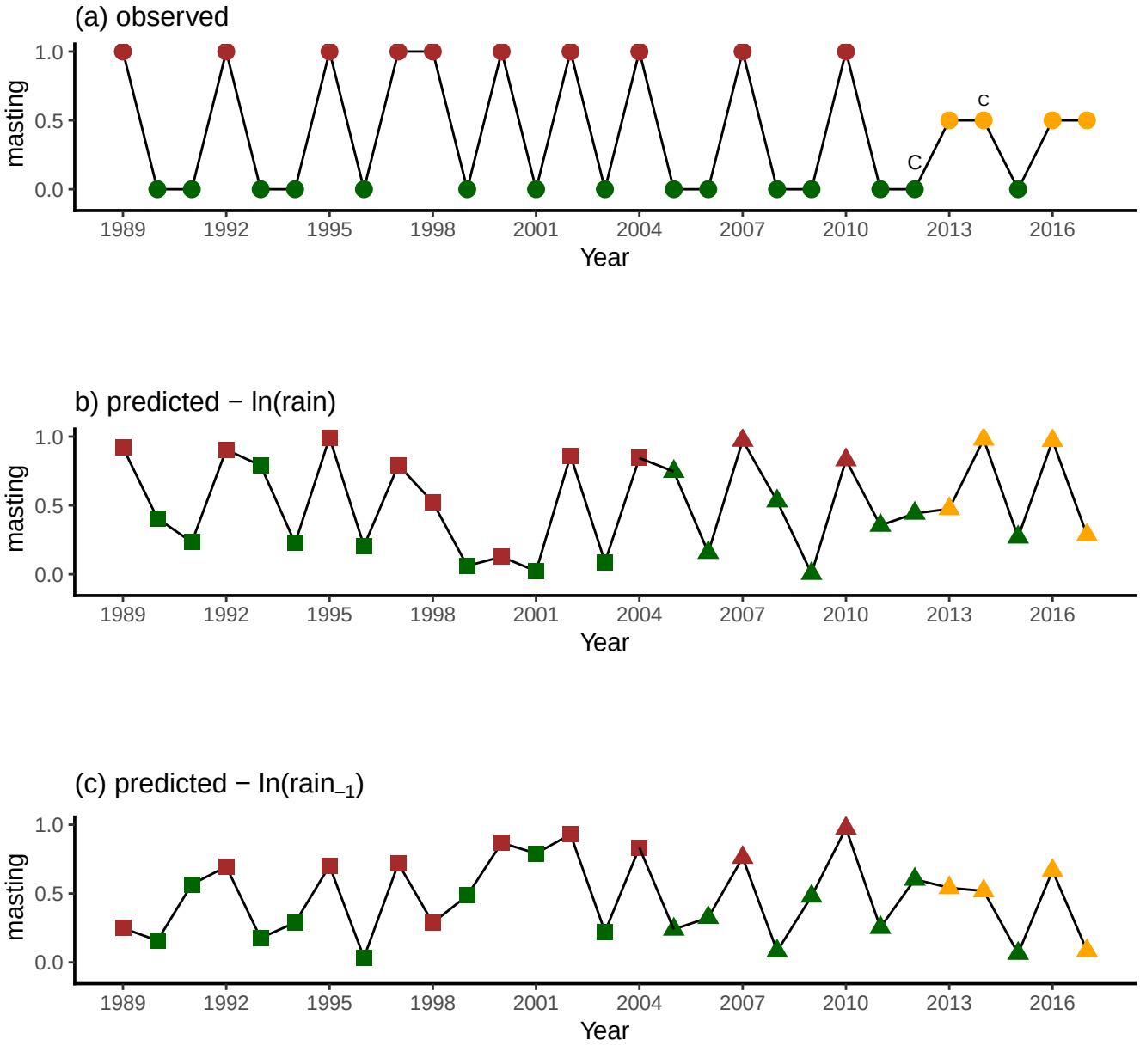
S5 Appendix. Rainfall and 30-day rainfall totals defining dry seasons.

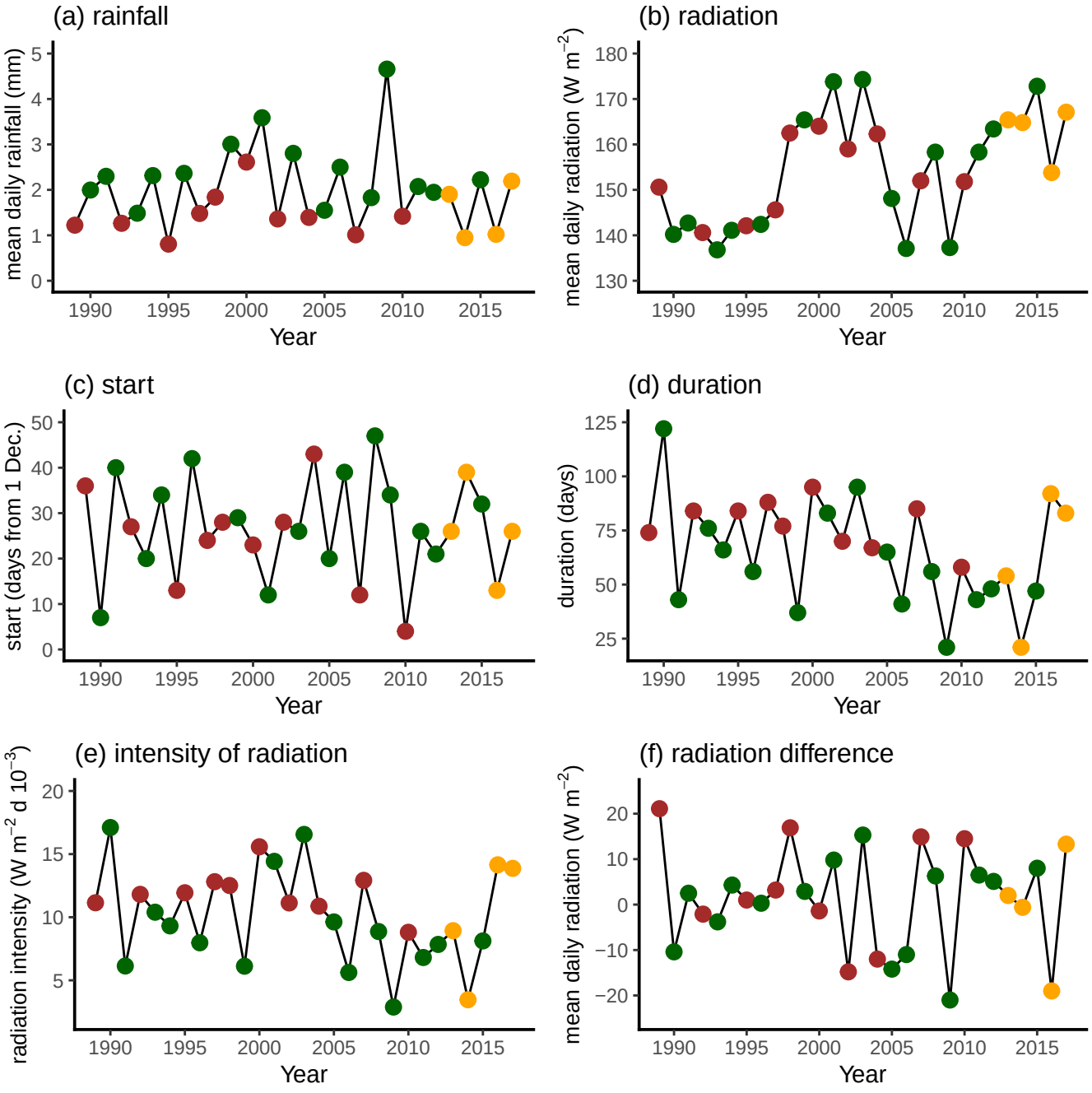
S6 Appendix. Description and feeding of the yellow-green caterpillar.

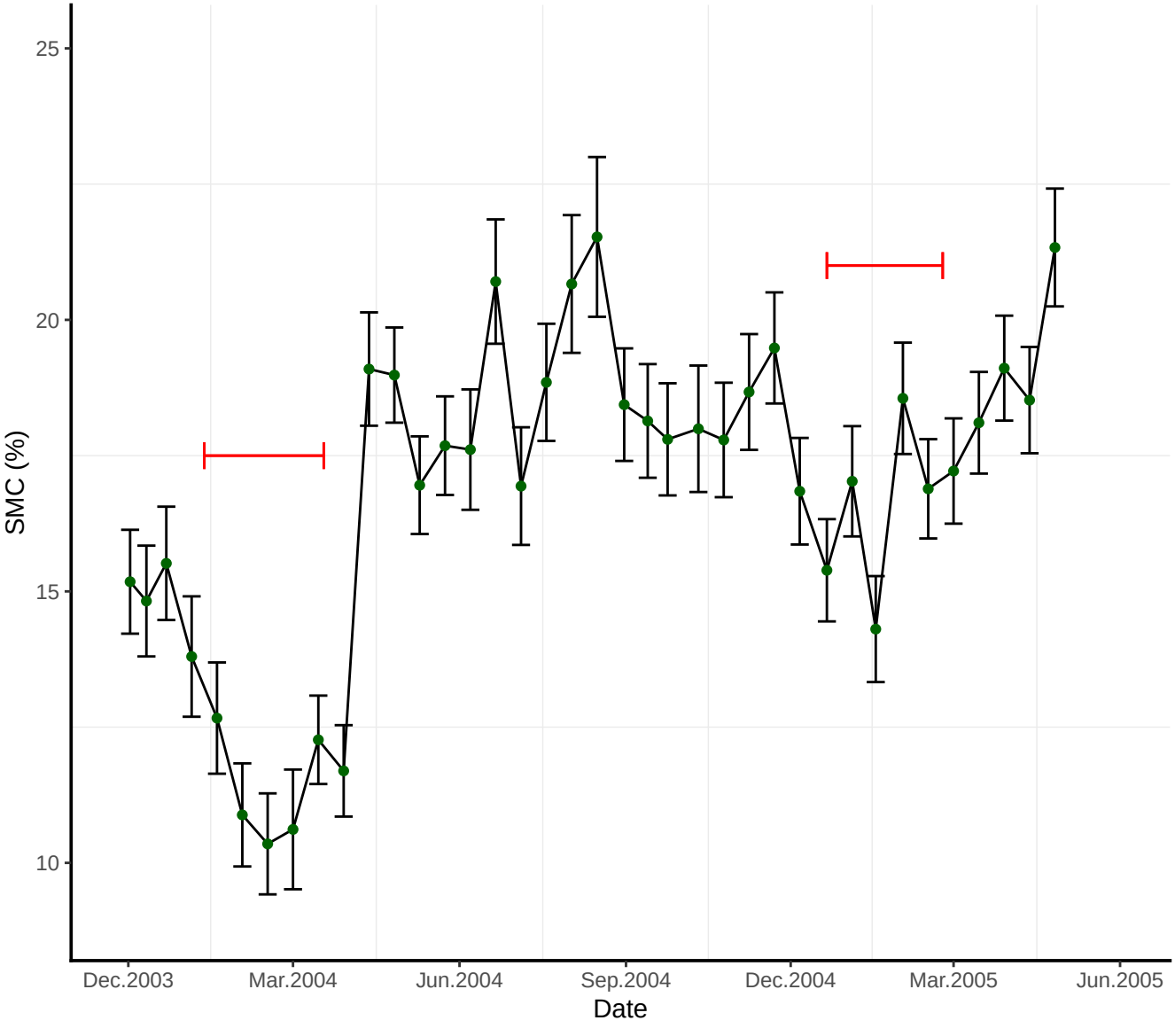
S7 Appendix. Analysis of Ndian PAMOL oil-palm plantation yields.

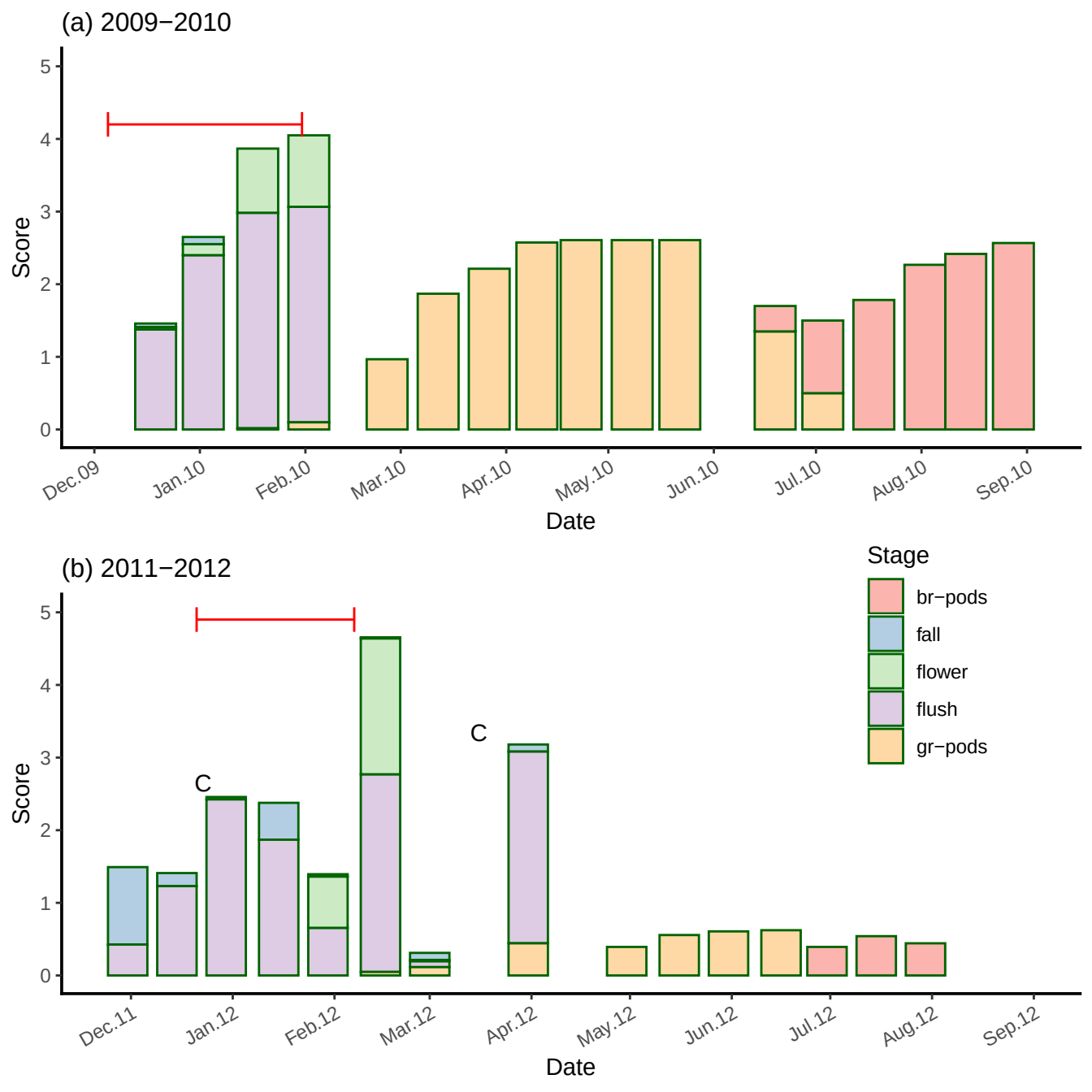
S8 Appendix. Stem increments from tree stem cores.

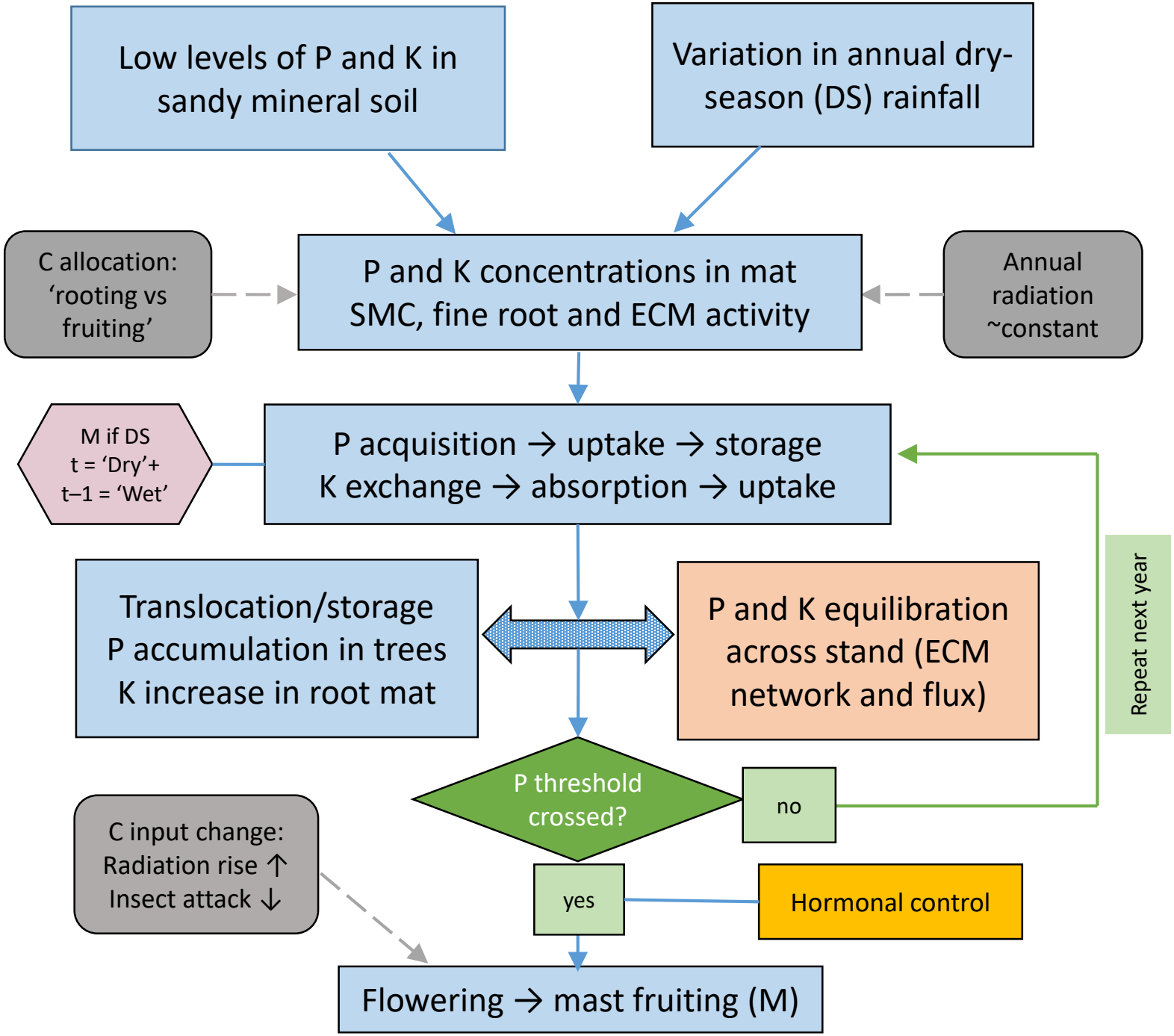
S1 Checklist. BPR Questionaire.


(a) observed
masting
1.0
0.5
0.0
C
C
1989
1992
1995
1998
2001
2004
2007
2010
2013
2016
Year
b) predicted − ln(rain)
masting
1.0
0.5
0.0
1989
1992
1995
1998
2001
2004
2007
2010
2013
2016
Year
(c) predicted − ln(rain$_{-1}$)
masting
1.0
0.5
0.0
1989
1992
1995
1998
2001
2004
2007
2010
2013
2016
Year


(a) rainfall
mean daily rainfall (mm)
Year
(b) radiation
mean daily radiation (W m^{-2})
Year
(c) start
start (days from 1 Dec.)
Year
(d) duration
duration (days)
Year
(e) intensity of radiation
radiation intensity (W m^{-2} d 10^{-3})
Year
(f) radiation difference
mean daily radiation (W m^{-2})
Year


25
20
15
10
SMC (%)
Dec.2003
Mar.2004
Jun.2004
Sep.2004
Dec.2004
Mar.2005
Jun.2005
Date


(a) 2009−2010
Score
0
1
2
3
4
5
Dec.09
Jan.10
Feb.10
Mar.10
Apr.10
May.10
Jun.10
Jul.10
Aug.10
Sep.10
Date
(b) 2011−2012
C
C
Score
0
1
2
3
4
5
Dec.11
Jan.12
Feb.12
Mar.12
Apr.12
May.12
Jun.12
Jul.12
Aug.12
Sep.12
Date
Stage
br−pods
fall
flower
flush
gr−pods


Low levels of P and K in sandy mineral soil
Variation in annual dry-season (DS) rainfall
C allocation: 'rooting vs fruiting'
P and K concentrations in mat
SMC, fine root and ECM activity
Annual radiation ~constant
M if DS
t = 'Dry'+
t–1 = 'Wet'
P acquisition → uptake → storage
K exchange → absorption → uptake
Translocation/storage
P accumulation in trees
K increase in root mat
P and K equilibration across stand (ECM network and flux)
Repeat next year
P threshold crossed?
no
C input change:
Radiation rise ↑
Insect attack ↓
yes
Hormonal control
Flowering → mast fruiting (M)