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

David M. Newbery[1*], Sarah Schwan[1], George B. Chuyong[2], Godlove A. Neba[2], Culbertson E. Etta[3], Julian M. Norghauer[1,4], and Martin Worbes[5]

[1] Section for Vegetation Ecology, Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland

[2] Department of Plant Science, University of Buea, POB 63, Buea, South West Region, Cameroon

[3] Research and Development Section, PAMOL Plantations Plc, Lobe Oil Palm Estate, PMB 3, Ekondo Titi, South West Region, Cameroon.

[4] Present address: Statistical Scientific Editing, Montréal, Québec, Canada

5 Tropical Plant Production and Agricultural Systems Modelling, Georg-August-University, Grisebachstraße 6, DE-37077 Göttingen, Germany

* Corresponding author david.newbery@unibe.ch

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Abstract

The large grove-forming tropical tree *Microberlinia bisulcata* (Fabaceae) is demonstrably a mast fruiter, and it is ectomycorrhizal. The Korup forest site in Cameroon has one short pronounced dry season; the soils are sandy and very low in P and K availability. Nutrients are largely recycled through a distinctive soil surface mat of fine roots and hyphae. Pods mature over the longer wet season after leaf exchange and flowering in the dry one. Reproductive allocation is considerable. 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 and possibly root grafts. 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 mechanistic explanation for the masting events observed.

Keywords Caesalpinioideae, 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 (Charlesworth 1980, Stearns 1992). Trees provide the large 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 economy, usually thought of as the teleonomic causes of mast fruiting and seeding: (1) the efficacy of fertilization may be increased by mass flowering, (2) seed predation may be more readily satiated by mass seeding, and (3) the chances of successful dispersal and establishment may be improved by larger reproductive output. The three processes are not mutually exclusive, they can happen together to different degrees and different times, and they could involve non-linear interactions. A model of an evolutionary stable strategy (*sensu* Maynard Smith 1972) for masting appears not to have been worked out so far: a suitable conceptual starting point could be the hypothesis of a serial adjustment of reproductive investment of Lloyd (1980).

Stochastic variation in weather conditions from year-to-year, interacting with site substrate conditions, very likely also play important moderating roles in masting. Kelly (1994), Kelly and Sork (2002), Crone and Rapp (2014) and Pearse et al. (2016) provide reviews of the now extensive literature in this field of study, covering the key concepts and hypotheses for masting. Much of the research reported has been in the ecological and evolutionary direction with a distinctly temperate-biome emphasis (e.g. for oaks, Koenig and Knops 2000). Beyond the dipterocarps in SE Asia (e.g. Curran and Leighton 2000), other studies in the tropics have been very few. More critical is that there still remains a basic lack of understanding of the underlying tree physiological mechanisms which enable mast fruiting and seeding to operate within an ecosystem. Together with the relevant environmental conditions, these mechanisms are sometimes referred to as proximate causes. What are viewed as proximate causes might in fact be the teleonomic ones as well.

For flower, fruit and seed production during a masting year to be allocated efficiently over the life-time of the adult tree, a physiological resource-mechanism must at least be in place. Budget models initiated by Isagi et al. (1997) 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 individuals (Abe et al. 2016, Satake and Bjornstad 2008, Vacchiano et al. 2018, Venner et al. 2016, Yamauchi 1996, Ye and Sakai 2016). This presents a restricted focus on the Moran effect. There may be more than one mechanism operating over time, or conceivably a mechanism changes in its functioning with ontogeny, depending on site and environment. Further, more than one resource might also be involved, affected by, and effecting, one or more plant hormones that control the cues and triggers which change a leafing axil into a flowering one, followed by fruit maturity (see

Marshall and Grace 1992). The individual tree is also probably best viewed as an integrated and dynamic system with regard to the intensity and timing of reproductive allocation. To move forward, more knowledge is clearly needed about the fundamental *modus operandi* behind mast fruiting. Exact mechanisms though can be expected to differ between species, forest types and biomes, each achieving an evolutionary stable strategy via different routes.

The evidence for C as the main resource directly involved in masting is weak. It comes from direct measurements of field trees, manipulations to branches on them in experimental ways, or alternative branch allocations; and from overall C budgets or studies on non-structural carbohydrates (NSCs) and their dynamics (Bustan 2011, Hoch 2005, Hoch et al. 2003, Ichie et al. 2013, Igarashi et al. 2019, Millard et al. 2007, Miyazaki 2013, Mund et al. 2010, Richardson et al. 2013, Sanchez-Humanes et al. 2011, Würth et al. 2005). Macronutrients have been suggested as potential key resources underlying budget mechanisms from just a few studies, but the evidence is scarce because this topic has been so little researched. Han et al. (2014) and Han and Kabeya (2017), for example, have shown that nitrogen (N) storage and mobilization is important for triggering flowering; and Fernandez-Martinez et al. (2017b) that P and Zn are likely involved in the mast fruiting of temperate forests. Carbon however should not be laid aside completely as a candidate resource as it likely operates in concert with N, phosphorus (P), potassium (K) or other elements, not just to build fruits and seeds but indirectly to grow and maintain other organs like roots for nutrient acquisition.

If macronutrients are behind the mechanisms of mast fruiting it would be expected that the element most important in control might be the one which is at lowest level of availability at the site, being that in most critical supply overall (Allen et al. 2017, Fernandez-Martinez et al. 2019). It will need to be accumulated to support reproduction, which in turn depends of attaining

110 the necessary stoichiometric ratios for seed filling, and doing so without undue costs to other tree
111 growth and maintenance demands in the short-to-medium term. This appears to be an extension
112 of Liebig's Law. In this way natural selection would be expected to evolve a cueing-threshold-
113 triggering system using this nutrient as a cell storage product. Other elements being in not quite-
114 such-low supplies, suggests a nested system of storage and thresholds with a similar structure.
115 Even so, the particular nutrient(s) could probably be different for different species, habitats and
116 biomes. The search then is for the key element(s) most determining growth rate of the trees and
117 controlling nutrient cycling, which then explain the frequency and intensity of reproduction in
118 each situation.

119 Artificial selection of trees for fruiting under controlled nursery conditions has given a
120 major insight into tree physiology with regard to fruiting and what may lie as the basis to
121 masting (Crawley and Long 1995, Davis 1957, Garcia et al. 2021, Monselise and Goldschmidt
122 1982). Cultivated trees often follow an 'alternating bearing' fruiting schedule, with years of 'on'
123 and 'off' harvests over a regular 2-year period. Several temperate trees in the Fagaceae
124 intriguingly show such an alternating pattern in natural forest, which leads to the idea that the
125 intrinsic minimal model is perhaps alternating years of reproduction across all masting species
126 (Newbery et al. 2006a), but in non-fertilized situations the interval between fruitings is extended
127 beyond 1 year to allow the time needed to accumulate resources and thus maximize fitness.
128 ('Interval' in this paper is defined as the years of non-masting, the time between masting years.)
129 Nutrients cycles have been implicated in several fruit tree studies (e.g. Rosecrance et al. 1996,
130 1998).

131 The hypothesis therefore stands that nutrients lie behind mast fruiting at the mechanistic,
132 tree-physiological, proximate level, and for many species, in particular species that are

133 ectomycorrhizal (Fagaceae, Pinaceae, Caesalpiniaceae, Dipterocarpaceae, etc.). It is testable and
134 falsifiable. Ectomycorrhizas (ECMs) may enable a form of economy of scale due to their large
135 shared mycorrhizal networks between tree roots equilibrating the levels of the limiting nutrient
136 resources (Newbery et al. 1998, 2006a). Both the tropical dipterocarps and caesalps are strongly
137 ectomycorrhizal and, more generally, masting in most temperate and tropical species is strongly
138 associated with having this symbiotic mode at the genus/family level (Newbery 2005). The role
139 of ECMs has been importantly overlooked in discussions of the causes of mast fruiting,
140 especially at the operating level of proximate factors (Corrales et al. 2018). A prime example of a
141 tropical ectomycorrhizal caesalpinaceous species which also shows strong mast fruiting is
142 *Dicymbe corymbosa* from Guyana (Henkel et al. 2005, Henkel and Major 2019). This and the
143 work of Green and Newbery (2002) and Newbery et al. (2006a) in a related study of
144 *Microberlinia bisulcata* in Cameroon were not considered by Pearse et al. (2016) though.
145 Outside of the impressive mass flowering events of the Dipterocarpaceae in SE Asia (see
146 Chechina and Hamman 2019), mast fruiting in the tropics has barely been recognized (Norden et
147 al. 2007).

148 There is a further aspect when considering how resources may affect reproductive
149 investment and schedules. In many cases, with the large dry mass allocations in masting events,
150 C is certainly involved, but it may not be a determining resource as regards reproductive timing.
151 Such high demands will mean that less C is available for root growth and root replacement, and
152 for stem and branch growth and maintenance, once the other key nutrient accumulated has
153 initiated the switch to fruiting (Kozlowski 1971). Accordingly, a secondary hypothesis advanced
154 further in the present paper, is that C is allocated more to these other tree parts in the interval
155 years between mastings. It will assist in nutrient acquisition in the case of roots, and in building

new wood and bark storage cells in the case of stems and branches, in preparation for the next masting. This is not to say that C and N (and K or other elements) would not be accumulated in the interval as well, but the accumulation of the more limiting (or controlling) element, say P in the case of caesalps, would probably be critical to the triggering. It would ensure that the elements are supplied in the stoichiometric proportions needed for the tree as a whole to move forward to successful fruiting.

An ecosystem that might test the nutrient resource limitation hypothesis best would be high-stature primary forest on soils low in one or two macro-elements, e.g. P and K, together with the supporting knowledge of focus tree growth, forest dynamics, nutrient cycling, soils and climate. A refugium affords the long evolutionary time span over which selection has occurred without the confounding effects of recent human disturbance. Such an opportunity is provided by the long-term work in Korup National Park. With these considerations in mind, the present paper builds on the study of mast fruiting in *Microberlinia bisulcata* A. Chev. between 1989 and 2004 (Newbery et al. 2006a) and extends it to 2017 (29 years). It tests and develops further the key hypotheses put forward in Newbery et al. (1997) and Newbery et al. (2006a), which are explained in the following section.

BACKGROUND AND CONTEXT

Given the strong indications that different sets of contingent factors can influence the mast fruiting of different species, it is essential to understand the site parameters, climate and forest type of each ecosystem in detail. The processes involved are all closely interdependent.

Microberlinia bisulcata dominates large patches or 'groves', 1-3 km across, in the primary rain forest of southern Korup. Trees ≥ 50 cm stem diameter attained 17.8% of the

178 overall density and 32.6% of total basal area in 2005, and together with co-dominants
179 *Tetraberlinia bisulcata* and *T. korupensis* correspondingly 46.5 and 61.3% (Newbery et al. 2004,
180 2013). All three species are strongly ectomycorrhizal as are several other co-occurring tree
181 species in the Detarioideae-Caesalpiniaceae within the Fabaceae (Newbery et al. 1988). They are
182 not N-fixing trees. *Microberlinia bisulcata* trees attain considerable stature in the main canopy,
183 characterized by wide dome-shaped crowns, and very extensive laterally-spreading buttress
184 systems (Newbery et al. 2009, 2013). The species is a leaf-exchanger and therefore semi-
185 deciduous: new leaves at the start of the dry season (December to February) push off the old
186 leaves, flowering follows within a month (Newbery et al. 1998, 2006a). Flowers are outcrossed
187 mainly by small bees and pollen seems unlikely to be limiting: bees are highly abundant in the
188 canopy during the dry season (Newbery et al. 1998). It remains untested, however, whether
189 insect pollination could form an economy-of-scale factor: in this connection presumably density
190 of trees plays a crucial role. Into the wet season (March to October) pods mature from soft green
191 to hard fibrous brown structures. Seeds are ballochoristically dispersed in August-September
192 (Norghauer and Newbery 2015).

193 The Korup-Ndian area along with Douala at the coast is climatologically special for
194 western Central Africa because it has one clear dry season each year as opposed to the two less-
195 distinct ones found elsewhere in the region. Site elevation is c. 80 m a.s.l. (range 50 to 100 m
196 south to north inland), slightly varying between swampy stream-fed lower areas up to local
197 slopes, in places strewn with quartzite rocks. The soils are very sandy and free-draining, acidic
198 and very low in available P and K (Gartlan et al. 1986), meaning that here high-stature tropical
199 forest is growing on one of the nutrient-poorest sites in tropical Africa. Within groves, soil
200 organic matter is largely confined to the top 2 cm of the profile, forming a surface mat that is

201 densely occupied by fine roots and mycorrhizal hyphae (Newbery et al. 1988, 1997). Larger
202 vertical roots are able to tap deeper water reserves. Nutrient cycling in the groves shows a 'fast-
203 forward' modus: leaf litter decay is fast, there is no permanent leaf litter layer, and most cycling
204 via the very efficient mat happens in the early wet season (Chuyong et al. 2000, 2002). At this
205 time throughfall nutrients help to prime decomposition and uptake (Chuyong et al. 2004). For the
206 rest of the year, heavy rains leach the forest, and this results in a tight closed ecosystem in which
207 ECMs play a central role in P acquisition and uptake (Newbery et al. 1997). In addition, annually
208 in the dry season, Harmattan dusts bring some P to the forest by aerial deposition. A critical field
209 experiment showed that growth and recruitment of *M. bisulcata* was not P-limited (Newbery et
210 al. 2002), presumably because of the highly evolved adaptations to the low-phosphorus site.

211 Recruitment of *M. bisulcata* over at least the last six decades has been poor due to very
212 low seedling and sapling survival (Newbery et al. 1998, 2000, 2006b, 2010; Norghauer and
213 Newbery 2010). Seed production in mast years is copious (Newbery et al. 2006a) but this
214 species' seedlings are strongly shade-intolerant (Green and Newbery 2001a, b). The groves
215 demonstrate transient dominance: the stands now are predominantly made up of large to very
216 large trees, with extremely few small ones present (Newbery et al. 2013). The dynamics is
217 thought to be one of patches arising and then decaying, being replaced, *in situ* or *ex situ*, within a
218 mosaic of species-richer forest (Newbery et al. 2013, Newbery and Gartlan 1996). The species is
219 classified as a long-lived light-demanding tree (see Newbery et al. 2010). Part of the expected
220 life-history strategy of long-lived and light responsive species such as *M. bisulcata* (Newbery et
221 al. 2010) would be to delay the size on maturity (SOM) in order that greater seed output later
222 offsets the relatively low probability of persistence in the forest understorey. Two further
223 coevolved traits are ectomycorrhizal habit and mast fruiting. Ectomycorrhizas not only provide

224 advantages in resource acquisition for juvenile and young adult trees but are also thought to be a
225 means to store resources which enable mast fruiting in the older adult ones (Newbery et al. 1998;
226 Newbery et al. 2006a). A key hypothesis is that these links, and possibly also root grafts,
227 between adults synchronize the timing of masts by equilibrating nutrient sinks across groves
228 (Newbery et al. 2000, 2010). There is increasing evidence from other forests that
229 ectomycorrhizas build intricate below-ground hyphal networks between individual trees (e.g.
230 Simard et al. 2012, Simard and Durall 2004).

231 *Patterns in time and first hypotheses*

232 Mast fruiting in *M. bisulcata* was first realized from early phenological recording in 1988
233 to 1995, with prominent seed crops in 1989, 1992 and 1995 and barely any seed fall in the
234 intervening years (Newbery et al. 1998). Flowering occurs to some extent in most years (a few
235 fail completely); and not always does a heavy seed crop depend on heavy flowering (Newbery et
236 al. 2006a). The two *Tetraberlinia* species tend to mast in the same years as *M. bisulcata* but not
237 both together (Newbery et al. 1998, and unpubl. data). After a propitious start with a potential 3-
238 year cycle for masting (i.e. a 2-year interval between mast years), this cycle turned out to be
239 shorter in the longer term. Because masting was associated with peaks in mean daily radiation in
240 the dry season prior to fruiting this suggested that C was at a premium, and some threshold
241 needed to be crossed before masting occurred. Detailed nutrient cycling studies in plots
242 dominated by *M. bisulcata* showed for the first time that leaf litter after a mast year (1989) was
243 low in P concentration compared with the years to either side, and this was matched by a decline
244 available P in the soil, especially in the surface organic layer (Newbery et al. 1997). This last
245 result suggested that P was being shunted into the seed crop and less was remaining to be shed in
246 litter, and given the low soil P at the site and the presence of ECMs, P was also likely limiting

247 mast fruiting. Tree C and P levels might be operating a double-threshold control system and this
248 led to the phosphorus and climate ectomycorrhizal response (PACER) hypothesis proposed by
249 (Newbery et al. 1997).

250 The climate at Korup varies stochastically from year to year, particularly regarding the
251 start, duration and intensity of the dry season (the dates defining the actual season each year
252 based on 30-day running rainfall total (*rft*) falling < 100 mm; Newbery et al. 2006a). This season
253 plus the first six weeks of the wet season very largely determine tree physiological processes for
254 the whole year. Fine-tuned sensing of the environment to optimize resource gain and allocation
255 within a life history strategy is central to survival. Under- or over-allocation at the wrong time
256 could lead to large fitness losses, hence the presumed operation of thresholds that safely trigger
257 phenological change. That C and P might be dual constraints within a broader nutrient-limitation
258 hypothesis as an explanation of mast fruiting for many tree species required a detailed budget to
259 show how much C and P (also N and K) were being allocated to fruits and seeds in a main
260 masting event. Censuses of seed and pod counts, their masses and nutrient contents were
261 achieved for the 1995 masting (Green and Newbery 2002), showing that *M. bisulcata* produced
262 on average 26K seeds per tree or 83.5K seeds/ha. Seeds are small (0.64 g each), and with an
263 average of 2.0 seeds per pod, total pod mass was 25 g (see images in Norghauer and Newbery
264 (2015: Appendix S1; at the 2007 and 2010 events 2.5 seeds per pod were estimated). Masting
265 resulted in an investment of 1034 kg /ha dry mass that year, and compared with leaf litter
266 production in previous non-mast years (Chuyong et al. 2000), was 52% of it by comparison, or in
267 a mast year 74%, i.e. a substantial allocation of resources (Green and Newbery 2002). Seeds and
268 pods together had N and P amounts 13 and 21% of that in annual leaf litter production, indicating
269 an important use of P during masting. 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* (Newbery et al. 2006a). 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 *more* intense than average (low mean daily rainfall), plus the dry season in the year prior was *less* intense than average (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 (Newbery et al. 2006a). What was perhaps important was the relative change in radiation between successive years 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 ECMs, coupled to nutrient transfers within the trees and ectomycorrhizal network (Newbery 2005, Newbery et al. 2006a). 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 extensio*, presents a more refined hypothesis and model of this remarkable phenomenon.

METHODS

Location

Korup National Park, in the South-West Region of Cameroon, is covered by primary rain forest of the Atlantic Coastal type (Letouzey 1968), and lies within the Guinea-Congolean refugium (Gartlan 1992). Phenological recordings were made in the main 'P-plot' located in the southern part of the Park (5º10' N, 8º70' E) at an elevation of c. 100 m a.s.l. (see Newbery et al. 2004, 2013). Mean rainfall 1984-2016 was 5159 mm (range 4023 to 6531). Access to the neighbouring oil palm estates of PAMOL Plc outside of the Park (Bulu-Mundemba, Ndian) allowed a comparison of their fruit yield with *M. bisulcata* mast fruiting with regard to climate variation. The estates have the same substrate and soil type as southern Korup but have received phosphate fertilization for several decades.

Climate

Climate data continued to be available from the PAMOL Bulu Station, Ndian (Etta et al. 2022). 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 (Appendix 1). 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 Appendix 1. 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 Newbery et al. 2006a) 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 series referenced in Appendix 1. World Climate data bases unfortunately proved quite inadequate for estimating these missing values due to the sparseness of regional stations in western Central Africa, the special topography around Mt. Cameroon, SSE of Korup, with the few data records available for the last decades being incomplete (see Appendix 1).

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 Newbery et al. 2006a); 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 being

338 shorter or longer. Hence, in what follows, 'dry season 1991' for example means December 1990
339 to February 1991 (modally). For a more general, less strict, annual matching of phenology to
340 climate, a 12-month year starting on 1 December one year and ending on 30 November the next
341 was adopted, with quarter 1 being December to February, and so on. Part-years were taken as
342 November to March (5 months, dry) versus April to October (7 months, wet) to encompass the
343 weeks before and after the dry season proper. Since its use in Newbery et al. (2006a), the
344 definition of drought dry season was slightly relaxed in that within the outer defining limits a
345 very few days where *rft* was at < 103 mm were counted in as drought days as long as the total
346 went back below 100 mm for the rest of the season. This affected four of the 16 years slightly in
347 their dry season durations and mean daily rainfall values (Table 1).

348 *Phenology*

349 The incidence of mast fruiting from 1989 to 2004 has been reported and analysed in
350 Newbery et al. (2006a). Recordings were accordingly extended anew from 2005 to 2017 for a
351 subset of trees, and it is the full time series of 29 yr that is presented and analysed in the present
352 paper. Evidence for masting rested on a mix of intensive phenological scoring of marked trees in
353 the two periods; quantitative trap-based estimates of seeding in two specific studies and from
354 which masting fruiting was inferred; circumstantial records linked to within-stand field seedling
355 experiments in some years, and general yet objective assessments of the whole forest in others in
356 the course of other experimental studies (Appendix 2: Table S1). Following pod maturity to
357 completion was not possible in 2017 because of security restrictions preventing access to KNP.

358 To increase the frequency of recording, between 1995 and 2000, 150 *M. bisulcata* trees in
359 the main 82.5 ha 'P-plot' (out of 294 in total with stem diameter ≥ 50 cm; Newbery et al. 2013)
360 had been scored on 61 occasions (mostly at monthly intervals), for intensity of leaf fall, leaf

361 flush, flowering and immature and mature pods (scale 0-3; Newbery et al. 2006a). Later, now
362 within an 8-ha sub-area of the 82.5-ha P-plot (1000-1200 m E, and 100-500 N, with respect to
363 SW origin; see Fig. 2a of Newbery et al. 2013), 61 of the 65 trees surviving since the last
364 enumeration in 2005 (stem diameter, mean ± SE = 112 ± 4 cm, range = 54 – 174 cm), were
365 scored between 2009 and 2013 in a similar manner as the first period. In 2014, fallen pod density
366 on the ground was taken as a proxy for mature pod density (Appendix 2, Table S1).

367 *Nutrients*

368 In an earlier litterfall study between May 1990 and June 1992, monthly bulked samples
369 from twenty 40 x 40-cm traps in each of 10 subplots were divided into two halves as set A, for
370 separation into fractions (leaves, small wood, etc.), and set B, for separation of just leaves into
371 the commonest 26 species (Chuyong et al. 2000). From this set B, leaves of *Microberlinia*
372 *bisulcata* were selectable and later – as for the other species – they were analyzed for N, P, Ca, K
373 and Mg concentrations. Leaflets and rachises were kept together. This species is a leaf-
374 exchanger, and has a very well-defined period of leaf litterfall annually, starting with onset of the
375 dry season (Newbery et al. 2006a). Subplots (each 40 x 80 m), were composed of five in low
376 (LEM) and five in high (HEM) ectomycorrhizal stands along the transect P in Korup (Gartlan et
377 al. 1986, Newbery et al. 1997). *Microberlinia bisulcata* occurred in only the HEM subplots, so
378 the number of replicate nutrient values per month was five. The 26 months were divided into
379 seasons according to the median rainfall pattern at Korup (as defined above), with those in the
380 dry season being generally December 1990 – February 1991 and December 1991 – February
381 1992, and the other months the longer wet seasons. Only dry seasons are considered here, and
382 nutrient concentrations for them were averaged across the three constituent months. A mast
383 fruiting occurred in (August-September) 1989, so dry season 1990-1991 is the second dry season

384 after the event, and dry season 1991-1992 the third one. The next masting was in the wet season
385 of 1992, so seen from this perspective the two dry seasons sampled were ~ 6 and 18 months prior
386 to the second event.

387 The opportunity to sample *M. bisulcata* leaf litter immediately after a later mast fruiting
388 came in the 2010-2011 dry season. A large system of over 400 seed traps had been used to
389 follow seed production and dispersal in the August-September 2010 masting (Norghauer and
390 Newbery 2015). These traps remained in place until early 2011 collecting leaf litter. The dry
391 season had started on 26 December 2010, and samples were taken on 29 January 2011. This
392 interval of ~1 month would have covered a very large proportion of the leaf fall of this species
393 that year, although the thin tail into February was not included. Thirty traps (from 68 small
394 clusters of the traps within 25 ha of the 82.5-ha permanent plot, Newbery et al. 2013) had
395 sufficient quantities of almost-only *M. bisulcata* leaves, lying in the traps as well-defined readily
396 collectable surface layers. Leaflets and rachises were separated on this occasion, and analyzed
397 for the same five elements as in 1990-1992, later recombining at the whole leaf level. The mean
398 dry mass ratio of leaflets to rachis in *M. bisulcata* leaves was 0.793:0.207, very close to 4-to-1.

399 In the dry season 1997-98 four traps of galvanized metal (same as used in 1990-92) were
400 compared with four similar ones but with hessian sack linings (used in the 1989-1991 study of
401 Newbery et al. 1997), each set being placed at random in each of the two quarter plots of six
402 HEM half-plots. Litter was collected over four consecutive fortnights between 21 December
403 1997 to 15 February 1998. *Microberlinia bisulcata* leaflets and rachises were again sampled
404 separately, dried and analyzed for N and P concentrations. Not all traps had sufficient material
405 and the replication per subplot/trap type/date ranged from 2 to 4. N and P values were successive
406 averaged for trap type, then subplot, and their weighted 4:1 leaflet-rachis averages found for the

24 date x plot combinations. Trap type had no effect on these two elements' litter concentrations (testing for Zn contamination had been otherwise intended). This litterfall was collected midway between a moderate double masting in wet seasons 1997 and 1998.

The 1998 masting event's seeds and pods, previously analyzed and reported in Green and Newbery (2002) for N and P, were analyzed further for K, Mg and Ca using standard acid digest methods and spectrometric determination (see e.g. Newbery and Neba 2019). To find the nutrient masses allocated to reproduction (fruits) and to compare them to the same used in foliage, seed and pod densities, together with leaf litterfall in another similarly strong (1992) mast year, were taken from Green and Newbery (2002). In these new calculations, mature leaf concentrations (for N and P) were used from a retranslocation study in Chuyong et al. (2000), which involved three dates: viz. December 1991, and April and July 1992. Litter fall dry mass would have been very slightly underestimating mature leaf mass because of some element retranslocation during senescence. Essentially, these leaf concentrations were from trees sampled on average 5 months before seed dispersal, and therefore concurrent with pod maturity that year.

In a separate study of litterfall by Schwan (2003), paired litter traps (same again as used by Chuyong et al. 2000) 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 2002-03 dry season came immediately after a masting in 2002, and next one was in 2004 (Newbery et al. 2006a). In this study only leaflets were analyzed for N, P, K and Mg.

Soil moisture

Soil moisture was recorded across two dry seasons to show that its variation could underpin soil nutrient processes which might be affecting mast fruiting, given also that *M.*

429 *bisulcata* trees have such very extensive lateral root systems close to the soil surface (Newbery et
430 al. 1997, 2009). On 2 December 2003, 12 soil moisture content sensors (Theta Probes ML2,
431 Delta-T Devices, Cambridge, UK) were installed in a stratified random manner across the
432 eastern 30 ha of the P-plot, one per block of 100 m x 250 m. Each probe was inserted
433 horizontally (at 40 cm depth, excepting three at 20 cm due to access problems) into a hole
434 excavated at the side of a small pit, the latter backfilled and packed down to the original density.
435 A subsample of soil from the excavated side hole was retained for fresh, water-saturated, and
436 later oven-dry weight (105 deg. C). With a hand-held meter, soil moisture content (SMC, %) was
437 recorded fortnightly until 26 April 2005 (38 times). Readings were repeated between 15
438 November 2006 and 15 March 2007 (nine times), with one last opportunistic recording on 29
439 January 2011. In the years 2004 and 2007 *M. bisulcata* had major mast fruitings, in 2005 and
440 2011 it had none.

441

442 RESULTS

443 *Mast fruiting cycle*

444 If masting is driven by availability of resources, and these are partly stochastic and partly
445 trending over time, then a full range of possibilities for interval length can be accommodated for
446 *M. bisulcata*. The extended time series (Fig. 1) shows that after 1995, as radiation increased
447 (Table 1), there was a double year 1997-98 with high seed crops, 1998 somewhat weaker than
448 1997, and then the interval dropped to 1 year (from a 3- to a 2-year cycle), with a masting
449 sequence 2000, 2002, and 2004, returned to very strong masts in 2007 and 2010 with a 2-year
450 interval, and then after that the control seemingly weakened to result in two pairs of consecutive

years, 2013-14 and 2016-17, which had moderate masting fruiting. The time series as it extended began to show increased non-stationarity, the first-detected period of 3-year cycling of 1989-1995 returned only once in 2004-2010: the regular cycle was seemingly just 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 of an intrinsic 3-year cycle. Because the time series is evidently non-stationary, any tests of randomization using techniques such as bootstrapping will not provide valid inferences (Cox 1981). Furthermore, bimodality will not be detected if the interval varies between 0 and 2 years.

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). After 2012 there appeared a new 'regime' of two sets of two consecutive years which showed only moderately strong ('m') masting. Logistic regressions were run with dispersion (φ) either fixed at 1.0 or allowed to be estimated (Agresti 2007). Whilst the latter gave marginally more significant fits, the former was adopted because the sample size was small and the estimation of φ would be unreliable (McCulloch and Nelder 1989). The models were therefore parsimonious and quite conservative with regard to Type I errors. Tree responses in each year were doubtless not fully independent from those 1 or 2 years before, being part of the inherent process of mast fruiting: the simple form of logistic regression did not account for temporal autocorrelation. With records for only *c*. 60 trees in common across all events, the sample was not sufficient enough to apply Monte Carlo subsampling to gain temporal independence. An event (masting = 1) was a composite outcome for all trees and, necessarily, it meant that almost all individuals were responding in a similar manner even though there was quite some variation in fruit production among individual trees.

Climate variation

Of the four basic climate variables, mean rainfall and radiation per day in the dry season, and start and length of the season (current year of masting and year prior) in Figure 2, only the first required ln-transformation to ensure too an evenness of X-axis spread in values of this independent variable. Extending the analysis to the full 29 years (1989-2017) required using the ordinal, or proportional-odds, logistic model (Agresti 2007, Fox 2008, Hosmer et al. 2013), where 'm' was scored as 0.5. Binomial and ordinal logistic models were run with the 'glm' and 'polr' commands in R (Fox and Weisberg 2019; Venables and Ripley 2002, package 'MASS'; R Core Team 2022), and in GenStat for comparison where also φ could be estimated (VSN International (2022). Given the modest length of the time series and data set, different models were fitted mostly with single independent terms, and when with two then the same variable with a 1-year lag, and only additively. No attempt was made to search for a best-fit subset model with interactions; if fact, most such model fits failed to converge when attempted. The binomial error distribution appeared satisfactory: the complementary log-log one as an alternative did not improve fitting.

Mean daily dry-season rainfall in years of full masting was lower than in those years' prior with no masting (Fig. 2a), with the exception of 2000, and if the averages of the rainfall values for the two double partial masting years are taken these are on a par with the masting ones. The time series for rainfall showed weak temporal autocorrelation (Appendix 3: Fig. S3a), 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 (Appendix 3: Fig. S3b).

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 (Appendix 3: Fig. S3c). 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 just significant ($P < 0.05$) at a lag of 3 years (Appendix 3: Fig. S3d). Radiation intensity showed a very similar pattern to duration (since radiation varied much less than duration) (Fig. 2e; Appendix 3: Fig. S3e). 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) was mixed with regard to masting response, although again a weakly significant negative autocorrelation for a lag of 1 year was evident (Fig. 2f; Appendix 3: Fig. S3f).

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 ($P < 0.05$), 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 $P < 0.015$ (Appendix 4: Table S1). 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 with ln-transformed variables also changed the significance levels very little ($P < 0.10$; Appendix 4: Table S1). 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 simpler binomial logistic ones (Appendix 4: Table S1 and Fig. S1) and, whilst significance decreased again using two-term models, they 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 Appendix 4: Table S2). 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 '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 the 'M' for 1998 and 2000 replaced by 'm', i.e. 1.0 by 0.5. The dependence of masting on ln(*rain*) in the current and prior seasons became slightly stronger ($t = -3.209$, $P = 0.0036$; $t = 2.913$, $P = 0.0074$, respectively).

Mast fruiting showed no significant dependence on mean daily radiation in the drought-defined dry season, in either the 1989-2012, or 1989-2017, time series (using binomial and

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

Radiation showed a distinctive long-term trend since the start of recording until 2017 (Appendix 3: Fig. S2), with the evident 11-year cycle. This was not related to change in instrumentation at Bulu (Appendix 1). Using a LOWESS regression fitting model in R ('lowess' command—a set of local smoothing splines, this trend could be removed and the differences between empirical measurements and the detrending curve then used as adjusted local year-to-year changes Appendix 3: Fig. S2a). The best result was with a span parameter of $f = 0.25$, which meant that radiation values > 1 year prior or ahead had some 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).

566 Lastly, to check whether heavy showers early in the dry season may have damaged
567 flowers or interfered with pollination success, mean daily rainfall was plotted across each year's
568 season. Of the 14 years with strong ('M') or moderate ('m') mast fruiting, ten had no showers of
569 ≥ 15 mm/day in the first 30 days, whilst in the 15 years without mast fruiting eight had no
570 showers ($\chi^2 = 3.55$, df = 1, $P = 0.060$), suggesting only a marginal tendency for mast years not to
571 have experienced potentially destructive rainfall events.

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

579 *Model predictions*

580 Using binomial logistic regressions of masting 1989-2004 on ln(*rain*) in the current and
581 previous years, fitted models were used to predict masting in 2005-2017 (Fig. 3), on the original
582 response scale of 0 to 1 (π; Agresti 2007). The series started at 1989, not 1987 as used in
583 Newbery et al. (2006a); and autocorrelation was not incorporated (see 'Time series analysis'
584 later though). The model fit for ln(*rain*) was good for the mast years 1989, 1992, 1995 and 1997
585 (marginal for 1998), and good for 2002 and 2004, but it wrongly indicated a mast in 1993 and
586 missed the mast in 2000 (Fig. 3a; fitted intercept [α] = 3.61 ± 1.80 and slope [β] = –5.77 ± 2.62, t
587 = –2.206, $P = 0.027$). Predictions of masting in 2007 and 2010 were very high ($\pi = 0.97$ and 0.83
588 respectively), and also that it did not occur in the intervening years. After 2012 though, one each

589 of the pairs of moderate ('m') masts was predicted as full ('M', $\pi = 0.98$ and 0.97). The predicted
590 masting in 2005 ($\pi = 0.75$) was incorrect, however.

591 With the model fit for ln($rain_{-1}$), 1992, 1995, 1997, 2000 [cf. with ln($rain$)], 2002 and
592 2004 were all well-fitting as mast years, but 1989 and 1998 were not: 2001 was fitted as a mast
593 year wrongly (Fig. 3b; fitted $\alpha = -2.47 \pm 1.40$ and $\beta = 3.96 \pm 2.00$, $t = -1.98$, $P = 0.027$). Again,
594 the model exactly predicted the mast years 2007 and 2010 masts ($\pi = 0.76$ and 0.97
595 respectively), and it managed three of the four 'm' years afterwards as being moderate masts
596 reasonably correctly. Therefore, similar to the outcome for cycles and intervals in mast fruiting,
597 the model fits were fair-to-good up to 2012 (the caterpillar-outbreak year; see later subsection)
598 but after that disorder and unpredictability ensued. Binomial logistic regression fits made with
599 the 1989-2012 data gave predictions (not shown) that were very similar to those for 1989-2004,
600 in the main because the mastings in 2007 and 2010 matched so well the time series to 2004:
601 yearly π-values (fitted and predicted) from the two runs were in very good agreement.

602 The median effective level of ln($rain$), that is the level when π (x) = 0.5 (defined as x = –
603 α/β; Agresti 2007) was 0.624, which back-transformed to 1.869 mm/day – a value very close to
604 the estimate for the ln($rain_{-1}$) estimate of 1.867 mm/day. This median level, which might be
605 interpreted as a form of threshold for non-masting and masting, applied well to the events and
606 their rainfall values in most years up to 2011 (Table 1, Fig. 2a) although ln($rain$) and ln($rain_{-1}$)
607 differed in a few years as being better or worse fitting and predicted. Years 2012, 2013 and 2014
608 had moderately high and quite similar mean rainfall in their dry seasons (1.90 – 2.07 mm/day;
609 Table 1) so aside from the caterpillar intervention, the rain threshold theory would not have been
610 expected to work too well—a form of counterfactual evidence. Afterwards, in 2014-2017, the
611 return to low high alternations in rainfall should, *ceteris paribus*, have led to 'M' heavy masting

612 in 2014 and 2017 (as predicted by the binomial logistic regression for ln(*rain*) (Fig. 3a), but it
613 still did not achieve that outcome.

614 *Time series modelling*

615 Times-series logistic regression—in full generalized logistic autoregressive moving-
616 average regression, with the command 'glarma' (package glarma, Dunsmuir and Scott 2015),
617 that accounts for temporal autocorrelation in binomial data (Cox 1958, 1981; Cox and Snell
618 1989, Dunsmuir 2016; McKenzie 1985, 2003), supported the binomial logistic regression results
619 for 1987-2012 even more strongly ($P < 0.01$ and $P < 0.05$ for ln(*rain*) and ln($rain_{-1}$) respectively,
620 for both lags p = 1 and 2, (Appendix 4: Table S1). Regressions using the time-series logistic
621 regression model for *radi*, $radi_{-1}$, *start* and $start_{-1}$ either failed to converge or the fits were
622 insignificant ($P = 0.17$ to 0.73). Whilst there was a weak positive effect on masting for duration
623 in the current year ($\beta = 0.041 \pm 0.025$, $z = 1.64$, $P = 0.10$), an even more strong negative effect of
624 duration was evidenced for the year prior ($duration_{-1}$; $\beta = -0.099 \pm 0.038$, $z = -2.62$, $P = 0.0087$)
625 (Appendix 4: Fig. S2). The last relationship analyzed before, with a binomial logistic model, was
626 only marginally significant ($P = 0.073$) so the evidence for the effect improved.

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

Radiation on quarter-year basis

Whilst a rainfall deficit delimitation will define the drought period in terms of limited water availability, it may not necessarily correspond precisely though to heightened radiation as well. 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 (Appendix 3: Fig. S1a). 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 ($P \geq 0.18$; Appendix 4: Table S3a), and also not for the other three quarters (Appendix 3: Fig. S1b-d; $P > 0.4$; 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; Appendix 4: Table S3a and Fig. S3; Appendix 3: Fig. S1e). Using again lowess smoothing regressions to remove trend in radiation (Appendix 3: Fig. S2b), with binomial logistic regression (1989-2012) masting weakly positively depended on differences in *radi* (P = 0.051), negatively though more marginally for $radi_{-1}$ ($P < 0.1$) (Appendix 4: Table S3b and Fig. S3). Time-series logistic regressions improved the fits especially for *radi* ($P < 0.02$), although only slightly for $radi_{-1}$ (P = 0.80). Fits to detrended differences (1989-2017) with ordinal logistic regression were intermediate in significance to those with binomial and time-series logistic ones

(Appendix 4: Table S3b). 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. (2006a).

An interesting feature of the LOWESS fits (Appendix 3: Fig. S2), 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 8 years lag (Appendix 3: Fig. S4a). In the third (JJA) and fourth quarters a similar but slightly weaker pattern for the function occurred, the negative lag now at 10-12 years (Appendix 3: Fig. S4b, c). 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 (Appendix 3: Fig. S4d).

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 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 (Appendix 4, Table S2a), these results for the 5-month season are 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 (Appendix 4: Fig. S4), 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 *inter alia* 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. 1). 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

704 radiation was changing proportionally. Radiation could have been sometimes high in the day and
705 rain fell at night: conversely radiation could have been low when there was cloud cover and yet
706 no rain, as was the case in some years at the transition to the wet season. Differences in
707 successive years' dry season radiation were more, respectively less, pronounced in the first and
708 second halves of the time series, for the DJF- than the drought-defined dry seasons.

709 *Tree size-fruiting relationship*

710 Scores for brown pods in 2007 and 2010 were matched with those for an equally strong
711 masting in 1995 on a tree-by-tree basis. Score categories '0' and '1' were combined. Fruiting
712 was significantly positively associated in both cases (χ^2 = 10.61, df = 1, P = 0.031 and χ^2 =
713 10.28, df = 1, P = 0.036, respectively). There is good evidence that high- and low-scored trees
714 tended to remain as such over a 12-15-year period, although considerable between-trees
715 variability existed. Ordinal logistic regressions of brown pod scores per tree versus tree stem
716 diameter (at last census in 2005), in 2010, 2012 and 2013, or as fallen pods in 2014, were weakly
717 and insignificantly related (t = 1.40, 0.45, –0.68 and 0.42, e.d.f. = 58 to 61, P = 0.17 to 0.60). As
718 the phenology score was recording the relative proportion of a crown fruiting, large trees did not
719 have proportionally more pods than smaller ones.

720 *Soil moisture content in dry season*

721 On graphing the time series for 2003-2005, three of the 12 sensors had three anomalous
722 and coinciding high peaks (~ 40 - <60%) in the 2004 and 2005 early-to-mid wet seasons
723 suggesting that their locations were prone to flooding. These sensors' data for the whole period
724 were accordingly omitted. Two of them were actually destroyed later by hunters. The time series
725 of mean SMC is shown in Fig. 4: 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. 4), 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 2003-04 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).

After the strong dry season of 2003-04, during which SMC reached a minimum of 10.4%, its values remained fairly constant at 18.24 ± 0.31%. The dry season of 2004-05 had much less influence on SMC (Fig. 4). 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 did not go either so low or remain low for long, and the match with SMC was weaker. At the start of the 2003-05 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 the 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 assumed free-draining locations. SMC before the dry season of 2006-07 was 20.7 ± 0.10%, and declined sharply and almost linearly to 14.0 ±

749 0.67% (*n* = 9 sensors), a difference of 6.7%. With the dry season that year lying within the span
750 of SMC recording dates, this last value was likely very close, if not at, the 2007 SMC minimum.
751 The mean value at 29 January 2011, a date also well into that year's dry season was 16.2 ± 0.8%
752 (*n* = 8, one sensor lost because its cable was chewed), a value close to that in the dry season of
753 2005 (Fig. 4).

754 The 30-day running rainfall total, *rft*, used to define the dry season in terms of drought
755 when this total goes below 100 mm, does not indicate either how much is the deficit, or how
756 steep is the decline into, or incline out of, the dry season. Appendix 5: Fig. S1 shows the course
757 of *rft* as the daily rainfall events occurred. The intense dry season of 2003-04 (2004 was a
758 masting year) resulted of *rft* going to zero, or very close to zero, for about 6 weeks (Appendix 5:
759 Fig. S1b), while in 2004-05 (2005 was a non-mast year) it was near zero for perhaps just 2
760 weeks, and shorter overall (Appendix 5: Fig. S1c). In 2002-03, for comparison, the also long dry
761 season *rft* reached zero for a couple of days, and whilst many days had no rain the season was
762 broken by three high rainfall events keeping *rft* just below 100 mm (Appendix 5: Fig. S1a). The
763 relatively small decrease in mean daily rainfall between 2005 and 2004 (Fig. 2) translated into a
764 surprisingly large difference towards the lowered SMC and suggested a non-linear effect, that is
765 a little less rain led to proportionally much more soil drying when rainfall was low-to-average.

766 *Caterpillar attacks*

767 In the latter half of December 2011, and again in the first half of March 2012, an
768 outbreak of a black caterpillar was observed that fed on young foliage of *M. bisulcata* trees
769 recorded for phenology in the P-plot. Although not quantitatively measured, the attacks were
770 extensive, as evinced by the substantial amounts of falling frass, numerous caterpillars hanging
771 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 (Norghauer et al. 2023). 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 (Norghauer et al. 2023). 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 (Appendix 6). 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 2010 and 2012

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. 5; Appendix 2: Table S1). 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. 5a), but was adequately captured for 2012 (Fig. 5b). The bulk

795 of the leaf-flush happened within each year's dry season, flowering well within it in 2010 but
796 coming at the end in 2012. Even though the sum of the flowering scores was similar in both
797 years, fertilization resulted in substantially more green and brown bods in 2010 than 2012 (Fig.
798 5a, b). Caterpillars were not seen in the other years between 2009 and 2013, notably not in 2010.
799 In 2010, green pods were apparent between 18 January and 3 July, that is for 5.5 months, with a
800 1-month overlap as they turned brown between 5 June and 28 August, over 2.5 months (Fig. 5a).
801 A similar time course was recorded in 2004 (Newbery et al. 2006a: Fig. 6), and likewise (for
802 green plus brown) in 1995 and 2000 (ibid. Fig. 5d). Interestingly the overall period of pod
803 formation was much shorter in the two back-back years of masting 1997 and 1998.

804 Trees in 2012 suffered unusually in two definite caterpillar attacks by the same black
805 *Achaea* species, both coming just prior to peaks in leaf-flush (marked 'C' in Figs 1 and 5). The
806 earlier flush in early January 2012 was part of the annual leaf exchange process, but the later one
807 in early April 2012 not. The first was in part associated with the leaf fall around 15 January
808 2012: 21 of the 61 trees lost new leaves then. The third leaf flush in late February 2012 (Fig. 5b)
809 had no associated caterpillar attack: what happened in late March was unfortunately not
810 recorded, but a building up of the re-flush starting then could be surmised if this event followed
811 the same flushing patterns of the earlier and later ones. The sequence of events suggests that leaf
812 flush in early January enabled the caterpillar population to initially increase, and that at the end
813 of February there was a response by the trees to the first attack. The flush at the end of April is
814 more difficult to explain. It could have been either a further delayed response to the first attack,
815 or a direct response to the second attack, by a possibly now larger caterpillar population. The
816 life-cycle dynamics of the herbivore would have allowed, however, only a second cohort of
817 caterpillars to feed on that third and last flush for the year. The most flowering accompanied the

818 middle leaf-flush peak in 2012, which speaks against caterpillars being around then because
819 feeding on leaves might be expected to indirectly reduce flowering.

820 The presence of the black caterpillar in 2012 appears to have upset the smooth stage-
821 replacement pattern of 2010, and led to a much reduced reproductive output. The interval from
822 the last year of full masting (1 year) was theoretically suboptimal, so likely the resource levels of
823 P but not N were reduced and still below a threshold. A high N: P ratio may have helped the
824 caterpillar outbreak. In addition, the masting pattern changed after 2011 (Fig. 1), to the two
825 moderate double-year form, possibly a carryover of the disruption of the feeding in 2012, and a
826 destabilization of the proposed inherent 3-year cycle. In the dry season 2010, mean daily rainfall
827 was 1.42 mm, yet the year prior it was 4.66 mm; correspondingly the rainfall for 2012 were 1.95
828 and 2.07 mm: prior-to-current ratios of 3.3 and 1.1 respectively. Interestingly, the lower
829 caterpillar activity noted in the other grove to the south was associated with average green-pod
830 score of 1.7 in May 2013 (n = 33 trees; Appendix 2), showing that masting was more intense
831 there than in the P-plot that year.

832 The second herbivore attack in January 2014 of the other unknown caterpillar species
833 was before the second of the moderate 'm' mast fruitings of the double-years 2013-14. Much less
834 is known about its effects particularly because detailed phenological recording did not continue
835 to end 2014. However, given that this species eats flowers, as well as young leaves (Appendix 6)
836 it most likely reduced the number of trees able to fruit that year, even if the outbreak was
837 contained to a far smaller known area than the successive outbreaks of the black caterpillar in
838 late December 2011 and early March 2012.

839 It is instructive, once again, to look at the course of rainfall events and *rft* during and
840 immediately after the dry seasons of 2009-2010 and 2011-2012 to find clues for the second, early

March, caterpillar attack. This last came during a second short dry period when there was that unusual third leaf flush (Appendix 6: Fig. S2c; cf. Fig. 5b). 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 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, late-starting and not so intense, dry season for a typical non-masting year (Appendix 6: Fig. S2b).

Palm-oil yield comparison

An analysis of the monthly yields of palm oil, for 2003 to 2016, from plantations adjoining KNP (Appendix 7), 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. Moreover, mast fruiting of *M. bisulcata* in this period (see Fig. 1 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 *inter alia* be used in an inverse estimation to confirm the interpolated missing months of radiation at Bulu in 2009-2011 (see Appendix 1).

Stem increment growth from coring

Annual radial increments (*incr*, mm) in stem growth of 20 cored *M. bisulcata* trees ≥ 50 cm diameter in the P-plot (see Newbery et al. 2013) were matched to occurrences of masting over the 15 years of 1989-2003 (Appendix 8: Fig. S1a). The end date was the last reliable year which had a reliably-determined annual band for all trees. Standard deviation increased linearly

863 with the mean over years (slope [CV] = 1.14, adj. R^2 = 50%, P = 0.002), indicating a
864 considerable variability in increment between trees in any one year (Appendix 8: Fig. S1b). No
865 masting was noted for 1988 (Newbery et al. 1997) but that is not fully certain.

866 Linear mixed-effects models were run using ln(*incr*) as the response variable, trees as
867 subjects (or 'blocks') and ± 'M' as the factor. A binomial logistic regression fit of masting versus
868 increment was not feasible as the power, with only seven events in the period, was low. There
869 were no significant differences for increment in either the current year (F = 0.79, df = 1, 279; P =
870 0.38), or in the year prior (F = 0.12, df = 1, 279, P = 0.72: increments available for 1988), or in
871 the year after (F = 1.90, df = 1, 259, P = 0.17). Thus larger respectively smaller increments were
872 not associated with current mast fruiting, not (by inference) caused by it, or conversely masting
873 did not cause a change in increment. Graphs of the increment series for each of 20 trees
874 individually (not shown) had no common correspondences with 'M' years, and the differences in
875 mean individual tree increment for fruiting type were highly inconsistent (+M: mean 2.49 ± SD
876 1.97, –M: 2.38 ± 1.98; differences 0.11 ± 0.77, range = –2.02 to 1.67). Mast fruiting appeared
877 little connected to stem growth increment in *M. bisulcata*.

878 Increment was positively correlated, however, with mean daily radiation in the typically
879 modal dry season period (using all records, i.e. 1984-2003), this 'quarter 1' being defined by
880 months DJF – (r = 0.507, df =18, P = 0.023), but not in the early and mid-wet season quarters 2
881 and 3 (P = 0.32 and 0.41), although again in late wet season 'quarter 4' it was (r = 0.479, P =
882 0.033). Fruiting would have been largely 50% over then, by mid-September. For the year as a
883 whole the correlation was also reasonably strong (r = 0.503, P = 0.024). Increment was not
884 strongly correlated with rainfall in any quarter, however, nor overall (P = 0.12 to 0.70), and not
885 with radiation in the year prior to masting (P = 0.10 to 0.73).

886 Binomial logistic regression fits of masting for 1989-2003 to mean annual core increment
887 with either *radi* or $radi_{sr}$ (current or prior year for both variables) were all insignificant for the
888 increment term (current: $P = 0.49$ to 0.63; prior: $P = 0.46$ to 0.95). The same approach applied
889 using increment of the year prior brought little improvement in fitting ($P = 0.18$ to 0.33; $P = 0.18$
890 to 0.62, respectively). Thus whilst increment and dry-season radiation remained significantly
891 positively correlated ($r = 0.532$, df = 13, $P = 0.041$), partialling out radiation effect was of little
892 avail in unravelling a fruiting-stem growth interaction.

893 *Nutrients and masting*

894 For 1997 and 1998, and for 2011, the leaflet-to-rachis ratio of N was 1.568 and 1.524,
895 and correspondingly for P it was 1.344 and 1.274 respectively, with means of 1.546 and 1.309.
896 For 2011 only the L/R ratios for K and Mg were 0.540 and 1.686. It was striking how much
897 higher was the K concentration in the rachises compared to leaflets.

898 In the 1990-1992 litter sampling the bulked samples each represented 0.320 ha of forest.
899 In 2011 sampling the trap clusters represented on average 0.368 ha. This means that each
900 nutrient value is similarly based on ~ 1/3 of a hectare, and the respective samples sizes of 5-and-
901 5 versus 30 can be retained in statistical comparisons without needing to group the 2011 ones.
902 Likewise, the 1997-98 study used some of the same half-plots, and accordingly had the same
903 scale as in 1990-92. Working with the typical masting cycle of 3 years shown by *M. bisulcata* at
904 Korup over the period 1989-2010 (Newbery et al. 1998, 2006a), the three sampling dates
905 together allow a series of immediately-after (2010-11), and 1 (1990-91) and 2 (1991-92) years
906 after (and thus also immediately before the next), masting events to be constructed. The two
907 consecutive years are likely temporally correlated, but the time difference between them and
908 2011 is large. The further data from 1997-98 present an interesting comparison in that masting in

909 1997 had evidently not prevented a repeat even the following year. Over the successive four
910 fortnights, concentrations of N were 18.69, 17.20, 18.58 and 18.63 mg g^{-1}, and those of P were
911 0.802, 0.799, 0.787, 0.956 mg g^{-1}.

912 The concentrations across the three weekly litter samples in December 2002 (Schwan
913 2003), were averaged per trap. To obtain whole-leaf concentrations, the averaged values per tree
914 were first divided by the 1997-98/2011 leaflet-to-rachis ratios to have indirect rachis estimates,
915 and then the 4:1 leaflet-to-rachis mass ratio was applied. This assumed that the ratios from the
916 1997-98 and 2011 studies could be used here for 2002 (which lay between them). For the
917 complete five-element data sets and direct estimation of leaf concentrations in Table 2 (viz.
918 1991-92 and 2011), years 1-3 after masting, N, P, K and Mg all differed strongly and
919 significantly (F = 13.4, 12.2, 27.2 and 6.01, all $P < 0.01$) but not Ca (F = 1.0, $P > 0.05$).

920 The results show that in the inter-mast period, N was low for the first two dry seasons and
921 then rose the year before the next masting, P increased from low to high approximately linearly
922 in the period, Ca barely changed, K and Mg were relatively high for the first two seasons but fell
923 in the third before masting (Table 2). This suggest that N and especially P concentrations were
924 depleted by the last mast fruiting and were re-instated before the next event. K and Mg increased
925 earlier in the interval but were presumably deployed elsewhere before masting. Despite the
926 different sampling approaches, standard errors of means, across years per element, were quite
927 similar. The concentration within the double-masting period 1997-98 intriguingly lay between
928 the 1991 and 1992 ones for N, but were higher than both of them for P. That P was accumulating
929 before masting is clearly demonstrated. The rise in P at the end of the litter fall series, but not of
930 N, in 1998 is also remarkable (Table 2). The 1998 litter was collected immediately before a
931 masting like the 1992 one, so they could be considered comparable in this respect even though

932 the previous mast fruiting events were 1 (unusually) and 3 years prior respectively. Averaging
933 the 2011 and 2002, and separately the 1992 and 1998, values where possible in Table 2 gives
934 composite estimates of leaf concentration respectively immediately post and prior to masting: N:
935 16.73, 18.80 (+12.4%), P: 0.615, 0.825 (+33.9%), K: 5.00, 2.44 (–51.1%), and Mg: 3.42, 2.53 (–
936 26.0%). These inter-mast changes suggest that N and P were depleted by fruiting and restored for
937 the next event—proportionally three-fold more for P than N, but the opposite occurred for K and
938 Mg.

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

946 *Microberlinia bisulcata* leaf litterfall rates in the 12-month July-to-June periods of 1990-
947 91 (non-masting in 1991) and 1991-92 (masting in 1992)—found by integrating the areas under
948 curves of litter fall versus time in Chuyong et al. (2000: Fig. 2d)—were practically the same
949 (1710 and 1670 kg ha^{-1} yr^{-1}, respectively). Multiplying these values by their corresponding P
950 concentrations (Table 2), led to a difference of 0.168 kg P ha^{-1} yr^{-1}, which is very close to 50%
951 of the investment in masting in 1998 (Table 3), assuming that the mast fruiting that year was
952 similar in intensity to the one in 1992.

953

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 (Newbery et al. 2013) and the varying climatic variables on all time scales ranging from years to decades and centuries (Nicholson et al. 2000, 2018). The inconstancy might be best understood with a two- or three-factor threshold model, where C, P and K reach potentially different thresholds, simultaneously or sequentially. Thresholds themselves may not even be constant over time but relate to age, climate trends, and other tree-internal demands. When one of the resources reaches its threshold early, its effectiveness could be limited by the slower accumulation of another resource. The first resource will need to be stored or allocated elsewhere in the tree, even to then support the faster acquisition of the lagging resource. In time the second resource accumulates to a level that crosses a pre-set threshold, and this then allows the first resource to come into operation.

976 The allocations of C to mast fruiting in *M. bisulcata* are substantial. The earlier mast
977 fruiting event of 1995, 28 out of 30 trees recorded had fruits. The average number of seeds per
978 tree was ~26K (maximum 92K). Using estimates of mean dry masses of seeds and pods, and
979 mean numbers of seeds per pod, the total dry mass investment was 17 and 307 kg per tree
980 respectively, summing to 324 kg per tree (Green and Newbery 2002). These per-tree masses
981 translate to 53 plus 981 = 1034 kg/ha, ~55% the mass of average annual leaf-fall (Green and
982 Newbery 2002). Applying the individual seed and pod masses to counts made for the 2007 and
983 2010 events, for trees that had pods (Norghauer and Newbery 2015), gave 181 kg per tree in
984 2007 and 122 kg per tree in 2010. (Excluding the two zero-producers, output values for 1995
985 were 346 kg/tree.) On this basis the investments per masting tree in 2007 and 2010 were 52 and
986 35% respectively of that in 1995, illustrating an up to almost two-fold variation in masting
987 intensity across these full fruiting events. Other more semi-quantitative scorings of mastings
988 across the rest of the time series suggest a similar range in reproductive output.

989 Flowering is a precondition to fruiting, but the dependence is not exact. Heavy flowering
990 was recorded in 1992, a mast year; but in 1991 there was also especially heavy flowering but no
991 mast fruiting (Chuyong 1994, Newbery et al. 1998). In 1990 there was some low fruiting
992 (flowering unmonitored), this coming though in the year after a main mast fruiting in 1989:
993 further, 1993 had very little flowering and consequently almost no fruiting, and 1994 relatively
994 high flowering but only scattered individuals fruiting Green and Newbery 2001a, 2002). From
995 the later, more detailed, phenology recordings, 1995, 1997, 1998 and 2000 had strong flowering
996 and were masting years, whilst 1996 and 1999 flowering was practically absent and had no
997 masting (Newbery et al 2006a: Fig. 5). Whilst valvate bracteoles protect flower buds before
998 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 (Newbery et al. 2006a: Fig. 6): 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 (Newbery et al. 2006a), masting remains also subject to any 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 developed any pods carried them through to maturity. The control of masting therefore most likely happens before flowering (see Newbery et al. 2006a for further discussion). After that seed failure is simply a chance unpredictable cost within the evolved life history schedule.

1022 *Nutrient resources — interdependencies*

1023 Analysis of the seed and pod nutrient concentrations and amounts in relation to those in
1024 mature leaves indicated ratios of between ~ 0.1 and 0.2 for N, P, Mg and Ca, but substantially
1025 higher at 0.6 for K. This difference is very largely due to the low concentrations of the first four
1026 elements, and a much higher one for K in the pods. Pods were collected recently fallen. Caesalp
1027 pods are hard and rather water-repellent for several weeks, so it is very unlikely they adsorbed
1028 much K coming down in canopy throughfall, or were they leached to any extent. Had that been a
1029 cause of an increase, then Mg should have increased too, yet it did not. Presently it is difficult
1030 though to explain why so much K was being invested in pods. The comparative leaf K values,
1031 coming admittedly from a retranslocation study where replication of bulked samples per date
1032 was small, do closely match those of mature leaves of plantation-grown *M. bisulcata* trees
1033 (averaging ~ 5.8 mg $g^{-1;}$ at ages of 13 to 18 years; D. M. Newbery unpubl. data). Whilst ECMs
1034 are strongly linked to P acquisition and uptake in the P-poor soils, K is also very low in
1035 availability at Korup (Gartlan et al. 1986), and the surface-soil root mat (with dense mycorrhizal
1036 networks) is an efficient collector of K (and Mg) coming down in throughfall (G. A. Neba, D. M.
1037 Newbery and G. B. Chuyong, unpubl. data). In plots at the same site, Chuyong (1994) found N,
1038 P, K, Mg and Ca concentrations of 13.8, 2.09, 6.41, 2.22 and 3.50 mg g^{-1} respectively in Mb
1039 seeds that fell in 1992. Pods were not separated in the 1992 general collections but 'all
1040 reproductive parts' in the HEM plots, those with high abundance of *M. bisulcata* had a mean K
1041 concentration of 6.04 mg g^{-1}. Although other elements in fruits were albeit a little higher than for
1042 *M. bisulcata* alone in 1998, the earlier data well confirm the K values of interest. Investing P in
1043 seeds would presumably be important to the survival of establishing seedlings up until they could
1044 become infected with ECMs and link into the mycelial network. Could it be that also K, not P

1045 alone—as for some time thought (Newbery et al. 1988, 2002), is a second key controlling
1046 element of masting in the Korup groves, or as several indications suggest P and K might act
1047 synergistically?

1048 The main pattern explaining the masting time series was the sequence of relatively wet
1049 dry season followed by relatively dry one. There was no evidence of water limitation to large
1050 trees in the dry seasons because of their ability to root deeply, so this points to a soil or nutrient
1051 factor governed by soil moisture content, in the upper soil layer where fine roots and ECMs,
1052 form a root-mat, are most abundant and active in nutrient cycling. What is it about relative
1053 dryness and wetness of the dry months that leads to these relationships? Possibly dryness
1054 affected the fine roots and ECMs. The drier the dry season, then likely the more restricted the
1055 root activity under limiting surface soil water conditions; which would possibly signal stored P in
1056 the ECMs to be moved to intermediate locations ready for fruiting, and less would be used in
1057 maintaining new root growth. In a relatively wetter dry season this root activity would continue
1058 longer and more effectively, so that any additional P stored in the roots would stay there and not
1059 be signaled away to fruiting. Nevertheless, the main mineralization and uptake occurs in early
1060 weeks of the wet season (Chuyong et al. 2002), and this would be similar each year once the
1061 water contents were high enough. This dryness then is thought to be a proxy for a mechanism
1062 that triggers translocation, but it is one that cannot operate without the previous year acquiring
1063 more P, and setting up a form of 'relay'. It is interesting that 'm' events occur in double-years
1064 and twice later, mirroring the two 'M' years 1997-98.

1065 At Korup in the HEM plots, sand, silt and clay proportions were 77, 9 and 14%
1066 respectively (Newbery et al. 1997). There exist very few published water content vs water
1067 potential curves for sandy loam tropical soils, but at a site in NE Brazil with a very similar

1068 physical composition to Korup, Fisher et al. (2008) found that a change in SMC (at 30 cm depth)
1069 from 20 to 12% (cf. the wet-to-dry-season change in Fig. 4) led to a decrease in soil water
1070 potential (SMP) from –10 to –100 kPa—which is very much higher than the generally accepted
1071 value of –1500 kPa where wilting starts. Such a translation across sites should however be
1072 treated cautiously because any SMC-SMP relationship is finely dependent on the exact physical
1073 composition of the soil (Or and Wraith 2002). Wilting of understorey treelet and shrubs, even in
1074 the strongest dry seasons, was very rarely observed at Korup. Nevertheless, the drying of the top
1075 surface soil with the root mat might still be expected to affect nutrient uptake capabilities in the
1076 dry season. In those dry months the surface leaf litter is definitely dried out, and in many places
1077 the sandy-loam soil just below the organic layer is visible which leaves the root mat exposed.
1078 The implied sensitivity of fine roots and ectomycorrhizas of *M. bisulcata* to surface soil water
1079 conditions might in part result from this species very pronounced buttressing and an extensive
1080 lateral root system lying just below the surface soil mat (Newbery et al. 2009).

1081 A cycle of 3 years would most likely allow a restocking of P, not only enabling growth of
1082 other tree parts, but also storage of P in wood rays and roots ready for fruiting (as the model later
1083 explains). A 4-year cycle could arise but ex hypothesis, that would need a sequence of two dry
1084 dry-seasons: none was recorded however. The regression modelling gave an indication that year-
1085 to-year increases in radiation, and positive deviations from the smoothed trend of radiation with
1086 time. Changes were relatively small, radiation varied rather little from year to year, both for the
1087 dry seasons and the years as a whole. The additional radiation probably did not contribute to
1088 much increase in photosynthesis which would cater completely for the extra demand in years of
1089 masting, above the potential competition for C by leaves, stems and roots. Variation also in start
1090 and duration of the dry season, with the fairly steady daily radiation inputs, meant that there was

1091 probably sufficient radiation supplying C on top of tree storage, to meet the high dry mass
1092 investment in fruits. Carbon supply was probably therefore not the limiting factor to masting.
1093 One way to resolve this possible contradiction is to propose that, internal to the tree, there was
1094 strong temporal division in the allocation of C between rooting (one year, more wet) and fruiting
1095 (the next, more dry). Further, the lack of a relationship between proportion of crown fruiting and
1096 tree size may be further evidence that C is not the primary limiting factor for mast fruiting (as
1097 was originally suggested by Green and Newbery 2002), if it can be assumed that large trees store
1098 more NSCs than small ones. The lack of year-to-year differences in oil palm yield relating to
1099 radiation is also moderate evidence of C from photosynthesis not being so critical for their
1100 yielding either. Palms can store up to ~20% of their C in stems from year to year (Corley &
1101 Tinker 2016, Legros et al. 2009). The lack of correspondence between oil palm yield and *M.*
1102 *bisulcata* fruiting suggests no common climatic driver and points to nutrients as the key factor in
1103 the unfertilized forest.

1104 The very few studies on C and nutrients involved in mast fruiting of dipterocarps that
1105 have been made largely support the thesis of this paper. Defoliation and girdling experiments on
1106 branches of *Dryobalanops aromatica* trees by Ichie et al. (2005b) indicated that flowering drew
1107 on C stored in local branches and the filling of fruits came from nearby leaves. This confirms the
1108 many similar conclusions for temperate trees mentioned in the *Introduction*. Relative allocation
1109 of P to fruits was shown to be higher than of C and N for of another masting dipterocarp,
1110 *Dipterocarpus tempehes* (Ichie et al. 2005a), again emphasizing the importance of P in
1111 reproduction, especially on P-poor tropical sites. During a different masting event for *D.*
1112 *aromatica*, Ichie and Nakagawa (2013) found that P concentrations in branch, stem and roots
1113 steadily decreased during flowering and fruiting (but not in twigs and leaves), N fluctuated

slightly (in all parts) and, whilst K decreased during flowering, it increased during fruiting (in 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. (2005) and Newbery et al. (2006a). 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. (2018) 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. (2015) 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. C 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 roots and ECM production. This would lead to an even stronger competition between rooting and fruiting, once stem growth is partitioned aside. That seedlings and saplings survive

very poorly close to adults, led to the proposal of a reverse drain operating towards the old adults especially in mast fruiting years, for P as well as for C (Newbery et al. 1998, 2006b, 2010; Norghauer and Newbery 2016).

Previous estimates of leaf litterfall were 1880 and 1380 kg ha^{-1} yr^{-1} in non-masting 1990 and masting 1989 respectively (the first estimate is used in Table 3), and came from Green and Newbery (2002), who in turn based their calculations on January-to-December, plot-level, leaf litterfall estimates given in Newbery et al. (1997). The 1990-92 data later indicated 39% of that litter was from *M. bisulcata* trees. This 0.74:1 ratio may have been an overestimate, because it used calendar year estimates which would have missed linking November-December litterfall with that in January to April prior to masting, and the newer 1990-91 species-specific data were more precise. Or, it simply reflects variation in litterfall, viz. 1380, 1880, 1710 and 1670 kg/ha over the four years 1989 through 1992, which suggests that C supply was likely again not to have played an important role in determining mast fruiting since in around one masting event there was an implied cost to leafing and around the other none. The fruit-to-leaf amount ratios and reproductive allocations percentages in Table 3 may well be ~10% lower than the true values, if the 1990-92 litterfall estimates did apply. The 1990-1992 data also display a small shoulder in May 1992, possibly the result of the last older leaves being exchanged for the new green pods.

Green pods stay on the trees for more than 5 months and therefore will contribute C to their structures and to developing seeds. This is likely an important source, and pods and seeds may indeed be almost autonomous in this respect. Pods are also held up high on the outer canopy edges where their photosynthesis is maximized (Norghauer and Newbery 2015). Bennett et al. (2011) reviewed the role of pods in their photosynthetic capacity, and Zhang et al. (2016) provide a detail analysis of C balance in pods of *Medicago sativa* showing the considerable C

inputs 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 ECM activity to enable the uptake of nutrients allowing nutrient uptake, and an allocation to fruits and seeds when cued probably lies at the basis to the masting cycle (part of this paper's main hypothesis). 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 an increase in radiation and extra C input, a next masting would occur after 2 years. If either P accumulation was limited the tree would wait until the next year, 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

1183 governs root growth and ECM physiology, and the later ones connect to the early wet season and
1184 the throughfall which primes the start period of optimal leaf litter decomposition (Chuyong et al.
1185 2002, 2004). A dry season may well limit root activity, and it also would delay decomposition:
1186 one which was short would only affect the former. On the other hand, a relative wet dry season
1187 will be expected to restrict rooting and ECM activity much less and encourage the earlier start of
1188 decomposition, both processes leading to better nutrient uptake into the trees. ECM activity
1189 doubtless plays a role in P uptake, and the regrowth and maintenance of the root mat itself
1190 determines the level of retention of K leached from the canopy and its uptake.

1191 An important aspect in connection with P-supply for fruiting, is how P is taken up and
1192 stored in inter-mast years. In the dry season of 1988-89 and 1990-91 there were pronounced
1193 peaks of P in fallen leaf litter in the HEM but not LEM plots (Newbery et al. 1997: Fig. 11a).
1194 This peak was absent in 1989-90, directly after the heavy mast fruiting. The HEM litter would
1195 have been composed of ~80% *M. bisulcata* leaves (Chuyong et al. 2000). In a relatively dry dry-
1196 season with likely more fine root and ECM die back than in a wetter one, P might be translocated
1197 out of these fine roots and ECMs, going into storage for fruiting. Taken together the integrated
1198 aspects of this P nutrient cycle do provide reasonably strong support for P storage and use
1199 leading up to, and during, the masting events.

1200 Another result providing important evidence for P-storage is from the comparison
1201 between concentrations and amounts in the years across masting intervals which suggests further
1202 that 50% of P in masting was coming from retranslocation of P out of senescing leaves a few
1203 months before, probably stored in branches; and by difference it might be deduced that the other
1204 50% was older and coming from local branch/wood storage built up in the prior 1 or 2 years, still
1205 within the interval. That result would fit with the notion of a temporary store for P and not all of

1206 the P needed for masting could be supplied in the current year alone. Rosell et al. (2020) in a
1207 study of a range of tropical tree species found the inner bark of branches was especially
1208 important for NSC storage and, although not yet tested, this may be where P is also held, ready
1209 for fruiting. Jones et al. (2019) indicate this as a possibility for premontane tropical forests.

1210 If P in leaf litter is relatively low in concentration after allocation to fruiting (Newbery et
1211 al. 1997, and new evidence in this paper), then the fast-forward cycling proposed by Chuyong et
1212 al. 2000) could be temporarily slowed because mineralization by saprophytic fungi would have a
1213 low P litter resource to decompose. Root activity would either need to become more intense and
1214 efficient to take up the now lower soil levels, or at this time the ECM activity would come more
1215 to the fore by not only accessing low molecular-weight organic P molecules efficiently but also
1216 by effectively reaching low-concentration inorganic P sources further way from roots. This
1217 impasse would strongly select for the several co-adapted root mat and ECM traits seen in the
1218 field in order to achieve restocking of P. The rise in P accumulated just before masting could
1219 lead to higher P in falling litter that year which on one hand would mean fast re-uptake but on
1220 the other appears to be a dissipative risk when the perceived strategy is to save P (in the tree) for
1221 immediate use in fruiting. However, the ECMs being part of the whole tree system, and cycling
1222 highly efficient, P is being 'saved dynamically' within the nutrient cycle. Also, N and K would
1223 in parallel complement C in stores — the latter benefitting from the small increase due to
1224 radiation enhanced photosynthesis, all three also needed for seeds and pods. That P was high in
1225 falling litter just prior to masting might furthermore indicate that P stores were quite full after a
1226 2-year interval, and some of that 'extra' P was also coming from root retranslocation.

1227 The analysis of mast fruiting in 1989-2004 (Newbery et al. 2006a) used 150 trees across
1228 the whole P-plot, but the later recording 2009-2014 used a subset of 61 trees in the eastern half,

1229 an area 100-500 N by 1000-1200 E, on the higher ground with denser stands and larger trees.
1230 The masting time series could potentially have been confounded then by sampling extent
1231 changing over time, because for the earlier half (1989-2004) it was found that masting was
1232 significantly stronger on the relatively higher and drier sites of this eastern part of the P-plot
1233 compared with the rest of the plot (Newbery et al. 2006a). Allaying these doubts, the full and
1234 strong mastings in the second half (2007 and 2010) were confirmed by seed trapping across the
1235 entire plot (Norghauer and Newbery 2015). The two double-years, in the second half of the time
1236 series, were only moderate mastings despite being at the more favorable topographic location.

1237 The very strong mastings achieved by *Dicymbe corymbosa* in Guyana are associated with
1238 pronounced ENSO peaks in radiation (Henkel et al. 2005, Henkel and Mayor 2019). However,
1239 this ectomycorrhizal caesalp, although phylogenetically very close to *M. bisulcata*, is unusual in
1240 that it reproduces annually also by sprouting, which must impose a considerable demand on C
1241 and nutrients for growth. For this reason, it might be conjectured that C stores are probably being
1242 continually used up and hence, to achieve a mast fruiting, a dependence on an additional boost in
1243 incoming radiation in those ENSO years would be necessary. Again, in contrast to most of
1244 African caesalps (including *M. bisulcata*), one other caesalp *Gilbertiodendron dewevrei*—which
1245 forms monodominant stands in Central Africa—also exhibits mast fruiting (quite unsynchronized
1246 spatially, and at irregular intervals) but its seeds are very much larger (~ 30 g; Hart 1995) so the
1247 mass allocated to reproduction is far more than for *M. bisulcata*. Compared with SE Asia and C.
1248 and northern S. America, the lack of a strong ENSO signal in C. Africa is pertinent (Camberlin et
1249 al. 2001, Poccard et al. 2000). Masting in dipterocarps may well be for different suite of factors
1250 from those controlling the caesalps, achieving an evolutionary stable strategy along an
1251 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 a chance 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 (Norghauer et al., 2023). The caterpillar attacks may have interfered with the accumulation of P and thereby interrupted masting in full, leading to the unusual 'm' double years. The evidence of an herbivore effect is strongest for fruiting in 2013-14 because of the detailed phenology data in 2011-12. It is tempting to suggest that something similar might have been happening in 2015 before the very similar masting pattern of 2016-17: 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; Newbery et al. 1998), but *M. bisulcata* trees are the greatest in size with a

near-zero mortality rate (Newbery et al. 2013). 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 (Nascimento & Proctor 1994, Maisels 2004). 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 reason for yellow-caterpillar given the extensive phenological monitoring of *M. bisulcata* (Newbery et al. 1998, 2006a; Norghauer et al. 2023). 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 into the early wet season when caterpillars would occur, and 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 (van Bael et al. 2004), or simply mounting abundance over years (Wong et al. 1990), is entirely 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* can 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 P accumulated 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. 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 the second 'M' year.

An interesting aspect is the feedback control that might operate by way of C going either into fine roots and ECMs, 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 ECMs. 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 ECM maintenance 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 (Newbery et al. 1997), 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, isolating reductionist approaches will 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 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 with a threshold switch for P, but gradual altering of the components over a 2-3-year cycle. For this to operate it is necessary to hypothesize a feedback from the C-depleted branches

1344 to the more C-depleted roots. With the fruiting sink removed, C should move from stems to
1345 roots. Whether this needs additional hormonal control is an interesting question. It remains a
1346 conundrum why 'in the background' to the rooting-fruiting axis, stem wood growth is positively
1347 correlated in a quasi-independent way with radiation. Stems may be seen as the storage
1348 stabilizers, being placed centrally between shoots and roots. As they grow they store and balance
1349 the terminal demands. The levelling adjustment of C between the first and second interval years
1350 could perhaps explain the lack of clear correlation between fruiting (and inversely rooting) with
1351 stem growth increment. The time sequence within the year is also important here. In the second
1352 (drier) year of fruiting, C is not predominantly *ex hypothesis* going to roots in the early wet
1353 season but more to stems for storage, and en route there for filling fruits later in the wet season.

1354 If radiation were to increase during an increasing part of a cycle or as a longer-term trend,
1355 and C were alone the limiting resource for masting, then fruitings would come closer together
1356 and this would defeat the putative economy-of-scale selection. In this respect a non-stationary
1357 time series offer advantages when matched to an also non-constant climate environment. On this
1358 basis it would seem also unlikely that C could be the key resource for *M. bisulcata*. Further, C
1359 available per tree will decrease with tree age after the point of maximum crown extension
1360 because of the higher respiratory loads incurred in maintenance of the whole tree. This may be
1361 connected with the observed crown thinning of the largest trees (J. M. Norghauer, unpubl. data).
1362 When seed production was substantial, in proportion to the high flowering per crown then there
1363 would be a deficit of C to fill pods, or pod production would decrease, or another cost incurred
1364 (e.g. at the roots or wood production). But the evidence was that in *M. bisulcata* the relative
1365 crown-cover with pods remained constant with size and, by broad inference, age. As a tree grew
1366 to have a larger root system with ECMs to maintain, to acquire P and retain K, so when absolute

pod and seed output rose then the demand for P and K would also. As with C and N, we can expect that P and K is stored in ‘quick-release’ forms in wood and back rays of the stem and the main branches. A phenomenon often remarked is of one part of a large crown flowering and fruiting more than the others, which could be explained by a correspondingly more active root system of the tree, and a matching storage of nutrients in the wood and branches, on that side. (See Newbery et al. 2009 for the strong crown asymmetry in *M. bisulcata*.)

The arguments going from the nutrient concentrations in fallen litter through to the possibly the trees building up and storing P and K before masting are tenuous because of the 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 (Newbery et al. 1997) partly because the retranslocation was less (Chuyong et al. 2000), and it was argued 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 leaf, dead root and

old-pod 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 ECMs to organic P. This reliability aspect might then favour P over K as the better controlling factor in masting.

Phosphorus storage and control

What could the likely form of storage of P in trees be? Since Bieleski (1973) the most likely candidate is inositol hexa*kis* phosphate (= phytic acid; $C_6H_{18}O_{24}P_6$). It has been shown many times to be the main storage form in seeds, and has been detected in stem and roots. It forms salts with Ca, K, Mg, Mn and Zn, and in soils occurs commonly bound to Fe. It occurs in 19 hexa-structures which are interconvertible (Raboy 2003). It is viewed as the most frequent P-storage form when P is in excess, that is in passive storage; the P is readily retrievable and mobilizable. Other molecules can have seven or eight atoms of P but seem less common (Raboy 2003). Inositol hexa*kis* phosphate is involved in cell metabolism, in ATP regeneration, RNA export and the repair of DNA. It is prominent in cell storage biochemistry, which may make it a candidate for *active* storage. However, so very little has been researched in this area, and accounts for trees are very sparse. A notable exception is the study of Kurita et al. (2017), showing P storage in *Populus alba*, followed by release in spring, and indicating perhaps a common function in many deciduous tree species. It is conceivable that the same mechanism could operate in seasonal tropical trees and even be a basis to P storage for mast fruiting species. How inositol hexa*kis* phosphate is linked to polyphosphate formation in roots and mycorrhizas, and comes under hormonal control remains unclear.

1413 In an experiment with *Eucalyptus grandis* seedlings, comparing low and high P media,
1414 Mulligan (1988) detected stored P in the form of esters and residual P (mostly phosphorus
1415 proteins), especially in roots, and more so the low P medium. The idea is that these stores buffer
1416 the plant (maybe actively stored), from there P can be mobilized and sent to other stores in the
1417 shoots. In a similar vein, Netzer et al. (2017) comparing mature *Fagus sylvatica* stands, one on
1418 high and one on very-low P available soils, found that in the latter P built up in roots in late
1419 summer, and from there was moved on to stem and branches, suggestive of at least two storage
1420 sites in a series enabling adaptation to the poor site. However, hardly anything is known about
1421 how P stores are internally controlled, or how hormones signal transfers of P (Rennenberg and
1422 Herschbach 2013), which could give even a lead as how P might be built up in stores in masting
1423 intervals, and once a threshold level is met how the switch to flowering is signaled.

1424 Much evidence points to senescence in leaves, and possibly also pod formation, involving
1425 cytokinins too (Marschner 2012). Chiou and Lin (2011) have proposed different hypothetical
1426 models for inorganic P being regulated by cytokinins and sugar levels. How these promising
1427 models can be extended to storage and release of P has yet to be worked out. The strongest
1428 candidate for the elusive 'florigen' is a now widely held to be a flowering locus T [FT-] protein,
1429 which again appears to be controlled by a cytokinin (Turnbull 2011). Cytokinins act at long
1430 distances and are bidirectional in their effects, both of which might hypothetically implicate them
1431 in inositol hexa*kis* phosphate metabolism and P storage. It remains likely that floral initiation in
1432 *M. bisulcata* takes place at the end of the wet season, before leaf exchange occurs in the dry
1433 season (see discussion in Newbery et al. 2006a). Earlier results on apple (*Malus*) trees suggested
1434 already that a two-way process of hormonal control could be operating (Davis 1957), and the
1435 idea that sugars and other NSCs destined for the usually stronger root sink (Goldschmidt and

1436 Golomb 1982, for mandarin (*Citrus*), and Hansen et al. 1982, for prune (*Prunus*)—on K-
1437 deficient soils) might be diverted to the flowering meristem sinks under the control of
1438 gibberellins (Sachs 1977). How exactly the 'switch' occurs remains obstinately elusive
1439 (Monselise and Goldschmidt 1982, and to the present day). The precise consistency of alternate
1440 bearing in *Pistacea* orchards has been questioned on statistical grounds (Rosenstock et al. 2010).

1441 *Active storage hypothesis*

1442 Storage of C as reserves in trees (stem rays, bark and branch wood) was widely seen in
1443 the past as being passive. The C was being made available for regular annual growth processes in
1444 ways that optimized the economy of the tree. (Zimmermann et al. 1971). Extending this idea to
1445 nutrients, Chapin et al. (1990) produced a systematic table for N and P, reserves of the latter
1446 featuring mainly as inorganic phosphate, polyphosphates, or phospholipids, leading them to
1447 conclude that dependence on mineral nutrients is likely much more pronounced than on C for
1448 reproduction. Sala et al. (2012a) argued that the build-up of NSCs in stores in trees might be
1449 acting as a buffer against stochastic variation in C inputs due to environmental stresses (e.g.
1450 drought, herbivore attacks), which as a bet-hedging strategy would insure against temporary
1451 collapses in maintenance and growth. The storage would need to be active, rather than passive,
1452 otherwise in the latter case it would be used up immediately in extra current growth. Extending
1453 this idea to mineral nutrients, Dietze et al. (2013) hypothesized that N, P and K might also be
1454 accumulated and stored to guard against periods of reduced nutrient uptake, stabilizing the
1455 internal nutrient cycles. Hormones might therefore control source-sink processes actively. The
1456 empirical evidence for active vs. passive control of C storage in trees still remains weak and
1457 unresolved though (Hartmann and Trumbore 2016). But where P and K especially are limiting
1458 growth, evolution of such an active mechanism could be of considerable evolutionary advantage.

1459 Mast fruiting imposes a quasi-unpredictable (partially stochastic) demand on mineral nutrients
1460 supplies, and therefore for P and K active storage would serve it well, particularly in sites where
1461 uptake patterns themselves are subject to environmental stochasticity (the intensity of the dry
1462 season at Korup, for example).

1463 *Nutrients in alternate bearing of tree crops*

1464 Studies of alternate-bearing pistachio trees (*Pistachio vera*) have provided several
1465 valuable insights into how tree nutrient balance changes between 'on' and 'off' years. Whilst
1466 fruiting depresses root growth in fruiting years, uptake rates from the soil remained similar. If N,
1467 P and K moved from uptake mainly to leaves and shoots in 'off' years, and to fruits in 'on' ones
1468 at 3-6-fold the investment compared with 'off'-year uptake, this implies that stores were being
1469 drawn upon (Rosecrance et al. 1996). Trees stored 7- and 14-fold more N and P respectively in
1470 'off' than 'on' years, mostly in branches, which also suggests active storage (Rosecrance et al.
1471 1998). Of what went into fruits in an 'on' year, 70% of N and P came from storage, and 30%
1472 from retranslocation. For N and P, storage forms are well known (e.g. phosphoproteins), but for
1473 K they are not. K would need to be intensively taken up in the 'on' years (study cited here was
1474 made on well-fertilized plots, however), despite the slower root growth, transported and used
1475 immediately in the fruits (Brown et al. 1995). Interestingly, K concentrations in pistachio are
1476 inversely related to NSC concentrations, because K is needed for sugar transport to the apices
1477 where fruits are being formed (Marschner 2012). If this last process applied to *M. bisulcata* at
1478 Korup, K would be taken up in the mast years and, assuming also it cannot be stored in roots or
1479 branches, the only other feasible (temporary) store would be outside the plant, this is as
1480 exchangeable forms held on soil colloids, built up in the wetter non-masting years (G. A. Neba,
1481 D. M. Newbery and G. B. Chuyong, unpubl. data).

1482 Picchioni et al. (1997) further showed, for pistachio again, that N and P were translocated
1483 out of the mature pericarp into the seeds of the same fruits, although K was not, which left the
1484 pericarp relative rich in K on fruit fall (harvesting). This could have been happening in *M.*
1485 *bisulcata*, and in this way explains the K-rich pods. Possibly as pods browned they too moved N
1486 and P to the seeds. K having achieved its role in aiding sugar transport (under the hypothetical
1487 hormonal control suggested) was then redundant as regards reproductive investment *per se*: the
1488 fallen pods would be leached much later by the end wet season rains, even some remaining until
1489 next year, and in this way returning the extra K to the forest floor and soil colloid sites.
1490 Returning to the question of possible CHO storage in 'off' years, direct estimates showed that
1491 very little of the stores laid down in those 'off' years (8%) contributed to the 'on'-year yield
1492 (Stevenson and Shackel 1998)—confirming again the general finding mentioned in the
1493 *Introduction*. Overall, the main evidence is in favour of nutrients plus hormones being the
1494 controllers of alternate bearing and, *in extensio*, masting.

1495 *Soil nutrient status*

1496 Nitrogen supply has been shown to be important for fruiting in *Nothofagus* (Smaill et al.
1497 2011). In either N-fertilized stands, or unfertilized ones when rainfall was high (allowing higher
1498 N mineralization), masting was enhanced, subject to a temperature cue also operating. Likewise,
1499 Leeper et al. (2020) showed in N-poor sites, that masting of spruce was less frequent and less
1500 intense than at N-rich sites. Cone production was positively correlated with soil N in the year
1501 prior, not the current one. Both studies found lagged N-effects, implying that N was being stored.
1502 Nevertheless, unravelling the causes is difficult because the better, wetter, conditions one year
1503 for N supply are not conducive to floral initiation, which depends more on warm drier ones
1504 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. (2012b) 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. (2012b) 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 nicely the main thesis of the current paper on *M. bisulcata*. The association with ectomycorrhizas was not mentioned in the review of Pearse et al. (2016).

Climate factors which affect nutrient resource availability driving masting was a central argument of the review of Allen et al. (2017). This underlying process is how economies of scale become operational: the predisposition of trees to avoid seed predation or increasing their flowering efficacy is enhanced by synchronization. Allen et al. (2017) made strong recognition of the role of ectomycorrhizas, building on Henkel et al. (2005) and Newbery et al. (2006). That either N or P (rarely both) are often limiting where ectomycorrhizas tree species are successfully dominant in forests, must place a high demand on these elements for seed production. A set of resource acquisition and storage traits that would benefit growth and defense in these nutrient-poor habitats generally would be expected to be channel-selected through evolution to support an optimal life history strategy (Allen et al. 2012). Different storage routes could be postulated to work in temperate vs. tropical systems where respectively N and P are the more limiting. The Korup work posits that resource synchronization can, in part, be achieved via a shared

1528 mycorrhizal network. Given the lack of support for C storage being important for mast fruiting,
1529 clearly the C budget model of Isagi et al. (1997) needs to be rethought in terms P uptake, storage
1530 and usage.

1531 Fernandez-Martinez et al. (2019) recognized that many mast fruiting species grow in N-
1532 or P-poor soils, or at least on sites where the demand for these elements is high. The authors rely
1533 on foliar N and P concentration data. There are two problems with this approach: firstly, from
1534 among the masting species some samples may be from mast years, others from inter-mast ones
1535 pulling the differences between masting and non-masting species apart; and secondly, many
1536 species well adapted physiologically to nutrient poor soils do have nutrient levels similar to those
1537 on richer soils, but display different nutrient dynamics. Again, the obvious association with, and
1538 role of, ectomycorrhizas was overlooked. Contrary to the claim of Kelly (2020), nutrients can be
1539 hypothesized to determine masting when their availability fluctuates, and tree nutrient
1540 concentrations are synchronized via the mycorrhizal network. Stronger competition between
1541 masting and non-masting neighbours need not be invoked (as proposed by Fernandez-Martinez
1542 et al. 2020): it follows from ecophysiological adaption of the masting species to their nutrient-
1543 poor conditions. From the nutrient-supply model the other economy of scale factors can operate;
1544 in the case of *M. bisulcata* this would probably be mainly to satiate seed predators.

1545 Janzen (1974) asked why the intervals between mast fruitings in dipterocarps are so large
1546 and irregular. That would not fit with resources like P accumulating to given common levels.
1547 Resources could doubtless be stored like NSCs, but not stored only for fruiting, and when not so
1548 used would be moved to other sinks such as roots. Dipterocarps form diverse mixtures of species
1549 in many forests, with their individuals spaced out among those of other ectomycorrhizal and non-
1550 ectomycorrhizal species. Thus the functioning of a shared below-ground network seems less

1551 feasible, especially when the fungal species differ across tree species. However, Janzen (1974)
1552 interestingly raised the idea that masting may have originated in species when they were much
1553 more clumped in the evolutionary past than they are today, growing as patches of near single-
1554 species dominating stands. If nutrient resources were more commonly distributed, shared and
1555 equilibrated within such patches in the manner postulated for extant *M. bisulcata*, and over time
1556 the tendency to clump by some species degenerated as they locally formed mixtures with other
1557 tree species, then the nutrient-threshold mechanism behind masting may have lost its
1558 effectiveness.

1559 Root grafts could potentially provide another means of nutrient transfer between *M.*
1560 *bisulcata* trees within groves. Soil surface grafts have been observed at Korup although as yet
1561 none anatomically investigated and mapped. Early field experiments on *Pinus strobilus* in North
1562 America by Bormann (1966) point to this as a real possibility. It was suggested that the process
1563 would mostly operate between large dominant trees of similar size to enable an equilibration of
1564 resources across trees. Many temperate and tropical tree species form root grafts (Larue 1952,
1565 Graham and Bormann 1966), often close to stems and among large roots, but there is also
1566 evidence for grafts between roots at greater distances when the species has long surface roots,
1567 e.g. for *Dacryodes excelsa* (Burseraceae) in Puerto Rica (Basnett et al. 1993), or among smaller
1568 roots well below the surface, e.g. in oaks (Saunier and Wagle 1965). The extensively spreading
1569 root systems of *M. bisulcata*, connected to large buttresses (Newbery et al. 2009), make the
1570 crossing of roots at 15-20 m away from stems quite feasible. Because grafts form as a result of
1571 physical pressing together of roots, the restricted vertical space of the root mat would likely also
1572 encourage grafts between medium to small roots, and in this way create a large multi-nodal root
1573 network. Apart from possibly providing increased resistance to wind-throw—which would not

be important for *M. bisulcata* given its strong buttressing, and temporarily supporting suppressed, damaged or dying neighbours, other advantages of root grafts have not been so obvious (Lohle and Jones 1990). However, synchronizing nutrient supplies between, and storage within trees, across whole clusters would clearly be beneficial and strengthen masting. Root grafts would moreover provide a strong 'platform' for the ECM network and faster local transfers. A role for root grafts enabling masting has recently been suggested by Noble et al. (2018) to part explain alternate bearing in pistachio in a year when pollination synchrony (the Moran effect) was relatively weak. The focus in this plantation study was on C as the putative resource being transferred.

More directly relevant to *M. bisulcata* was the work of Yli-Vakkuri (1953) cited by Bormann (1966), showing that P was moving across root grafts of *Pinus sylvestris*: the last author made no connection to ECM status of pines or association of ECMs with mast fruiting (see Newbery 2005 later). Conceivably, ECM and grafted root-networks might operate together within *M. bisulcata* tree clusters, either contemporaneously or in successive phases around the end of the dry into the early wet season. If hormones are also transportable across grafts, an added level of synchronizing control is afforded. The role of tree root interconnections (ECMs and grafts) becomes an essential auxiliary to the main masting hypothesis. Bormann (1966) advanced the thesis that root grafts established first by alignment of xylem tissues which rerouted water flow and, later, connecting phloem tissues permitted organic and nutrient transfer. Between the mid- and late-ontogeny stages, *M. bisulcata* trees growing in dense patches become large adults, as described by the transient dominance model (Newbery et al. 2013), 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

1597 supplies, the root mat had fully formed, the litter nutrient cycle was stable, and P (and possibly
1598 K) were by then in greater demand for growth and reproduction. To know whether or not
1599 codominants *Tetraberlinia bifoliolata* and *T. korupensis* graft below ground onto *M. bisulcata*
1600 would be interesting. That the three species do not usually mast synchronously suggests, though,
1601 that they probably do not form interspecific connections as predicted by Graham and Bormann
1602 (1966).

1603 *Role of environmental stochasticity*

1604 Dynamics simulation models involving storage and thresholds, resource-switching in a
1605 randomly varying environment, yet with no economy of scale operating, are able to generate
1606 masting cycles when either the variation is strong (i.e. very good vs poor years occur) or, when
1607 the variation is not so strong, there is an increasing non-linear response to the positive variations
1608 (Fernandez-Martinez et al. 2017a). Even then masting can be diluted over successive years and is
1609 not quite bimodal. Under weaker variation in the environment an economy of scale is needed to
1610 achieve a well-defined masting cycle (Kerkoff 2004, Lyles et al. 2009). Such large differences
1611 between very good and poor years in terms of resources (assuming linear responses) are
1612 ecologically rather unrealistic though for medium-length time series covering fairly regular 2- or
1613 3-year masting cycles. This in turn suggests that without an economy of scale a non-linear
1614 response is more likely to be involved. An essential requirement of such masting would be to
1615 avoid degeneration of the time series into chaos—as shown by the models of Rees et al. (2002).

1616 The systems view would postulate a feedback control to avoid such chaos but it could
1617 allow for an unpredictable mix of 1-, 2- and 3-year cycles over time to the same effect in
1618 thwarting predator tracking. For a limited resource like P, such a system means regulation of
1619 internal fluctuations across the tree parts within a masting cycle, so that some equilibrium in the

1620 P dynamics is maintained medium-term. An economy of scale which itself involves a mechanism
1621 for P distribution would facilitate masting when based on storage and thresholds of that same
1622 resource. In this respect, ectomycorrhizal networks, which enable P acquisition and uptake (and
1623 possibly P storage), could bring about an equilibration of P across the connected roots of
1624 neighbouring trees, which would allow a contemporaneous storing and triggering of mast
1625 fruiting, as P levels rose in concert across all trees in the population. In the case of *M. bisulcata*
1626 in this study, the key climate variables vary in a somewhat normal way, and it is unlikely they
1627 can cue masting in a simple directly-linear manner. However, if wetter dry seasons lead to non-
1628 linear increases, or pulses, of P-and/or K-uptake, coordinated across the forest, synchrony is also
1629 possible. The network idea would also explain why one or both *Tetraberlinia* species often mast
1630 fruit along with *M. bisulcata*, because they largely share the same mycorrhizal species (Newbery
1631 et al. 1988, 2000). The non-stationary aspect of the main hypothesis suggests a finely-tuned
1632 evolved ecophysiological system in *M. bisulcata* allowing it to respond to variation of the
1633 climate in order to maximize its fitness.

1634 *Conclusions*

1635 The results in this paper confirm and extend the findings based on those for 1989-2004
1636 presented in the Newbery et al. (2006a) with greater statistical detail and confidence. It would be
1637 valuable to know whether the 3-year cycle returned after 2017. Post-dispersal predation is
1638 currently important, especially in well-lighted gaps although not in the shaded understorey or
1639 below *M. bisulcata* crowns. It could have been much more common in the past when either *M.*
1640 *bisulcata* individuals were scattered across the landscape (Newbery and Gartlan 1996), or when
1641 transient grove dynamics was at a stage of rebuilding (Newbery et al. 2013). Since, seeds and
1642 seedlings need P to establish and reach to the network of ECM, it would be evolutionarily

1643 advantageous for an ECM species to mast fruit and increase its chances of establishment. It is
1644 interesting that masting is achieved in the most clustered caesalps, and was not apparent for the
1645 more spatially dispersed species in southern Korup.

1646 Most of the C dynamics models for trees to date (e.g. Cannell and Dewar 1994, Lacointe
1647 2000, Makela et al. 2008, Franklin et al. 2012) do not cater adequately, if at all, for
1648 environmental stochasticity or non-constant reproductive allocation schedules. Source-sink
1649 models for herbaceous plants, let alone for more complicated trees, have made little conceptual
1650 progress in the last three decades since Farrar (1993), Kozlowski (1992), Minchin and Thorpe
1651 (1996), and Wardlaw (1990), apart from raising an unresolved debate over passive versus active
1652 storage. They usually assume steady-state equilibrium conditions, are often teleonomic (e.g.
1653 Thornley and Parsons 2014), and are strongly focussed on stem diameter growth and maximizing
1654 tree yield. They are, therefore, still too far away from an understanding of trees in natural forest
1655 ecosystems (see Le Roux et al. 2001) to explain even reproductive schedules like masting.
1656 Source-sink relationships, within trees especially, turns out to be very complicated: a more
1657 integrated systems approach is probably required. An important challenge is working out how P,
1658 K and N interact with C dynamics over the complete life-history schedule of a tree. A very
1659 interesting hypothesis coming from this extended phenological analysis is that both K and P
1660 levels might synergistically control mast fruiting of *M. bisulcata*, mediated by the physical
1661 structure and functioning of the surface root mat for nutrient cycling. To test this hypothesis
1662 further requires much more detailed recording of nutrient processes at the tree-level and within
1663 the system, replicated over several mast fruiting events.

1664 The fundamental driving variable behind the deterministic mechanically-intricate system
1665 operating to cause mast fruiting in *M. bisulcata*, is the stochastic variation in rainfall. 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.

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Author Contributions

DMN conceived and led the research, wrote the first full draft of the paper, developed the hypotheses, and performed the statistical analyses. GBC and CEE contributed to the climate data

collection and instrument calibrations, and CEE provided access to the oil palm yield data. GAN and JMN provided information and analysis of the herbivore events. SS provided data and input on the nutrient estimates. MW undertook the tree coring and stem increment measurements. GBC, GAN, SS and JMN all at different stages assisted with phenology recording. All coauthors commented and approved the final draft on the paper.

Conflict of Interest None.

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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): the '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.* (2006) for 1988–89 to 2003–04. The exception to note is the updated radiometer calibration equation applied (Appendix 1) which changed the scale (linearly) for radiation. The new radiation values for 1989–2004 are also in Appendix 1.

Year/dry season	Masting event	Start (days from 1.12)	Duration (days)	Mean daily rainfall (mm)	Mean daily radiation (W m^{-2})	Minimum temperature (°C)
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.

2169 Table 2. Mean (± se) concentrations (mg g^{-1}) of the macro-elements in leaf litterfall of *Microberlinia*
2170 *bisulcata* collected in the dry season immediately following the mast fruiting of 2010, and in the second
2171 and third seasons following the earlier masting of 1989 (t).

$t_{>mast}$	(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

2172

2173 [a], Schwan (2003); [b], Chuyong (1994) and Chuyong et al. (2000).

2174

2175

2176 Table 3. Concentrations of the five macro-elements in fallen mature seeds and pods (= fruits) of *M. bisulcata* collected during the 1998 masting
2177 event, together with concentrations of the same in mature leaves of this species collected in the same year of a previous (1992) event.

	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

2178

2179 [a] as reported in Green & Newbery (2002; Table 1); [b] mature, green leaves, from Chuyong *et al*. (2000; Table 6); [c] using estimates of oven-dry mass
2180 per ha from Green and Newbery (2002; Table 1): seed, pods and fallen litter: 53.1, 981.1, 1880 (kg ha^{-1}) respectively; [d] RA = fruit density/(fruit +
2181 leaf densities).

2182

2183

2184 Legends

2185 Fig. 1. The time series of mast fruiting of *Microberlinia bisulcata* at Korup, 1989-2017. Symbol
2186 colours: brown, full; orange, partial; and green, no; masting event recorded. 'C' marks the year
2187 2012, in the dry season of which the strong caterpillar attack occurred, and 'c' the one in 2014
2188 which was a smaller more localized attack.

2189 Fig. 2. Times series of the dry season climatic variables associated with the masting series: mean
2190 daily (a) rainfall and (b) radiation; (c) start date (from 1 December of year prior) and (d) duration
2191 of the season, i.e. that which preceded the masting event; (e) radiation intensity (= radiation x
2192 duration$\cdot 10^{-3}$); and (f) the difference in radiation ($radi_d$) between successive years (current minus
2193 prior). Symbol colours: brown, full; orange, partial; and green, no; masting event.

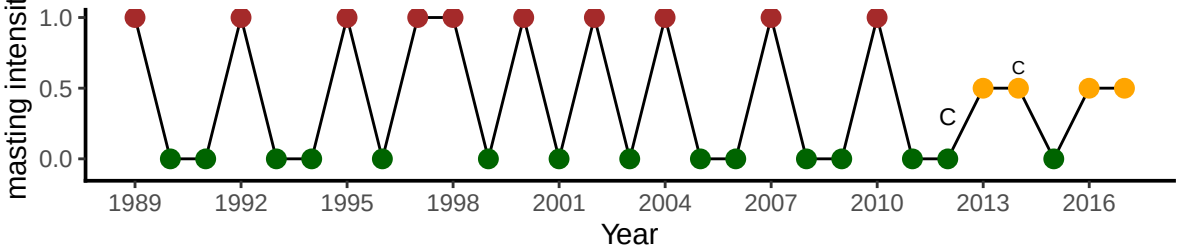
2194 Fig. 3. The probability of masting as fitted for 1989-2004 (squares), and predicted from 2005-
2195 2017 (triangles) using binomial logistic regressions of masting on the logarithm of rainfall in (a)
2196 the current, and (b) prior, year's dry season. Symbol colours: brown, full; orange, partial; and
2197 green, no; masting event recorded.

2198 Fig. 4. The course of soil moisture content (SMC, %), shown as means and SEs, at (mostly) 40
2199 cm depth, for 2003-2005 at Korup. The horizontal red lines indicate the span of the dry season
2200 for each year (see also Appendix 5: Fig. S1).

2201 Fig. 5. Changes in the mean scores of five phenological stages of *M. bisulcata* trees at Korup in
2202 (a) 2009-2010 and (b) 2011-2012. Stages: leaf fall (blue), leaf flush (purple), flowering (green);
2203 immature (yellow) and mature (red) pods. The horizontal red lines indicate the span of the dry
2204 season for each year (see also Appendix 5: Fig. S2).

2205

Fig. 1


masting intensity
1.0
0.5
0.0
C
C
1989
1992
1995
1998
2001
2004
2007
2010
2013
2016
Year

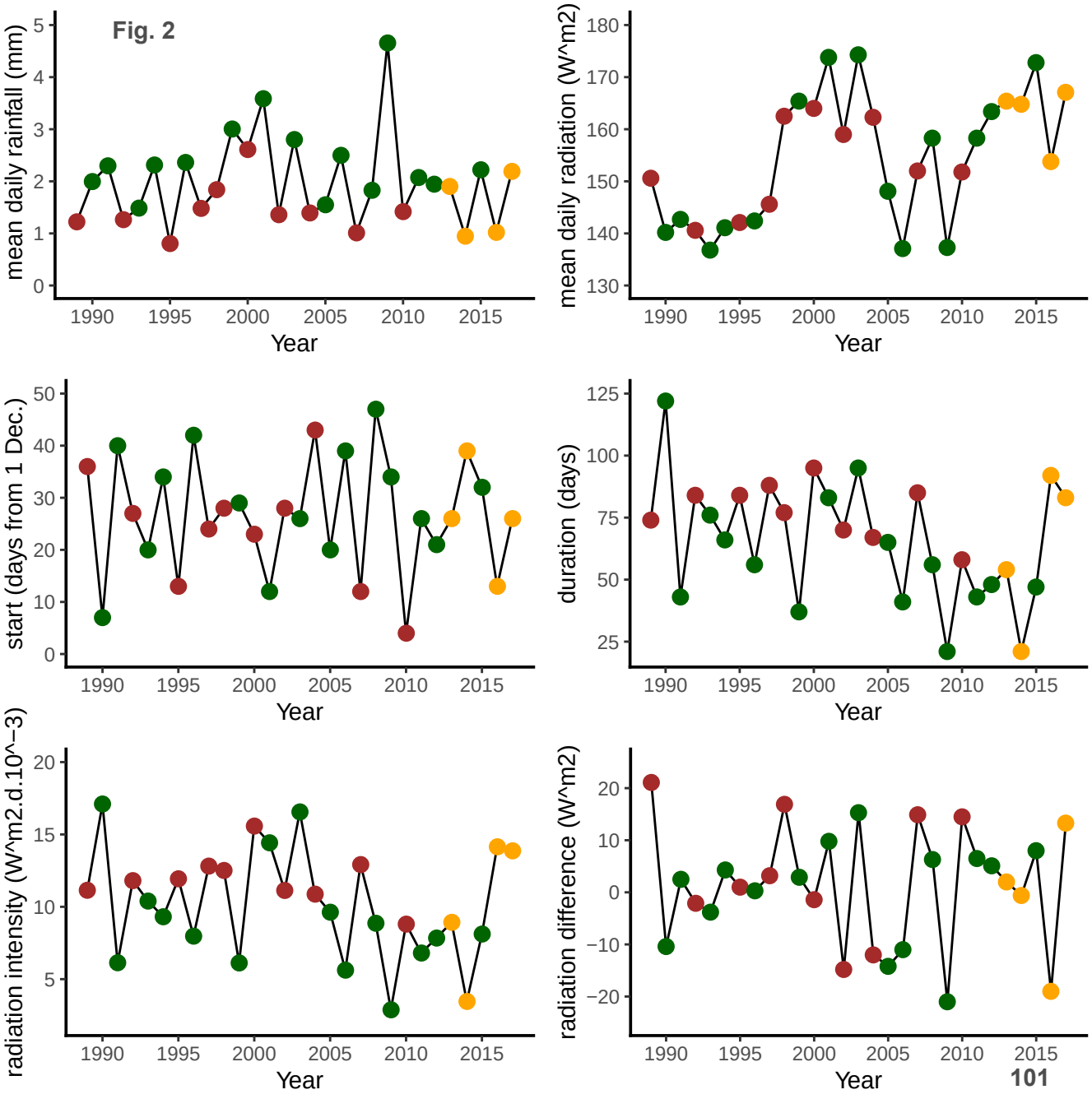
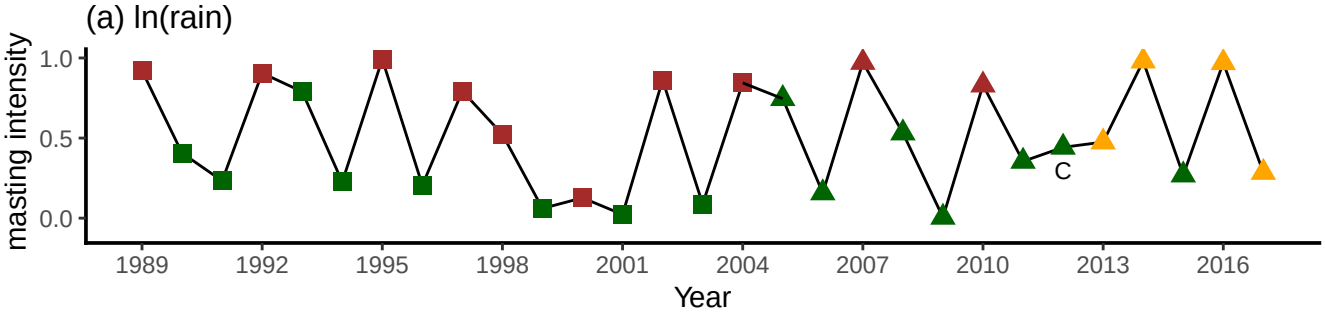


Fig. 2
mean daily rainfall (mm)
mean daily radiation (W^m2)
start (days from 1 Dec.)
duration (days)
radiation intensity (W^m2.d.10^−3)
radiation difference (W^m2)
Year
1990
1995
2000
2005
2010
2015

Fig. 3


(a) ln(rain)
masting intensity
1.0
0.5
0.0
C
1989
1992
1995
1998
2001
2004
2007
2010
2013
2016
Year

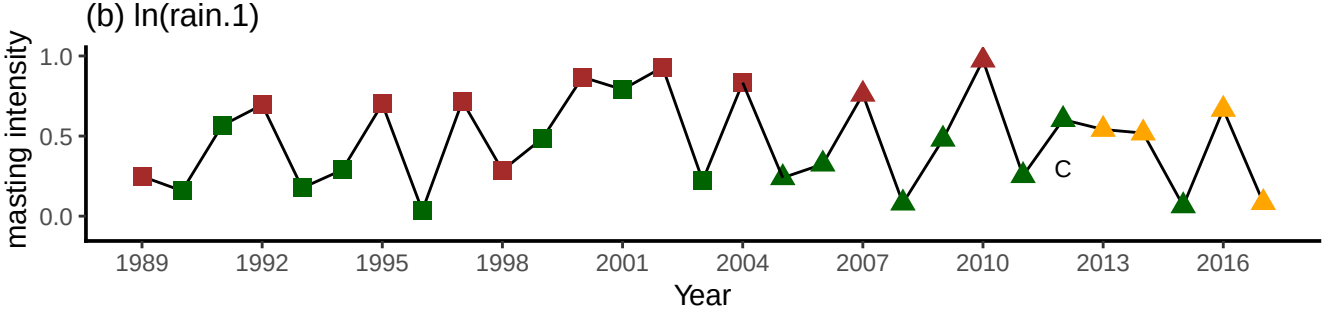

(b) ln(rain.1)
masting intensity
1.0
0.5
0.0
C
1989
1992
1995
1998
2001
2004
2007
2010
2013
2016
Year

Fig. 4

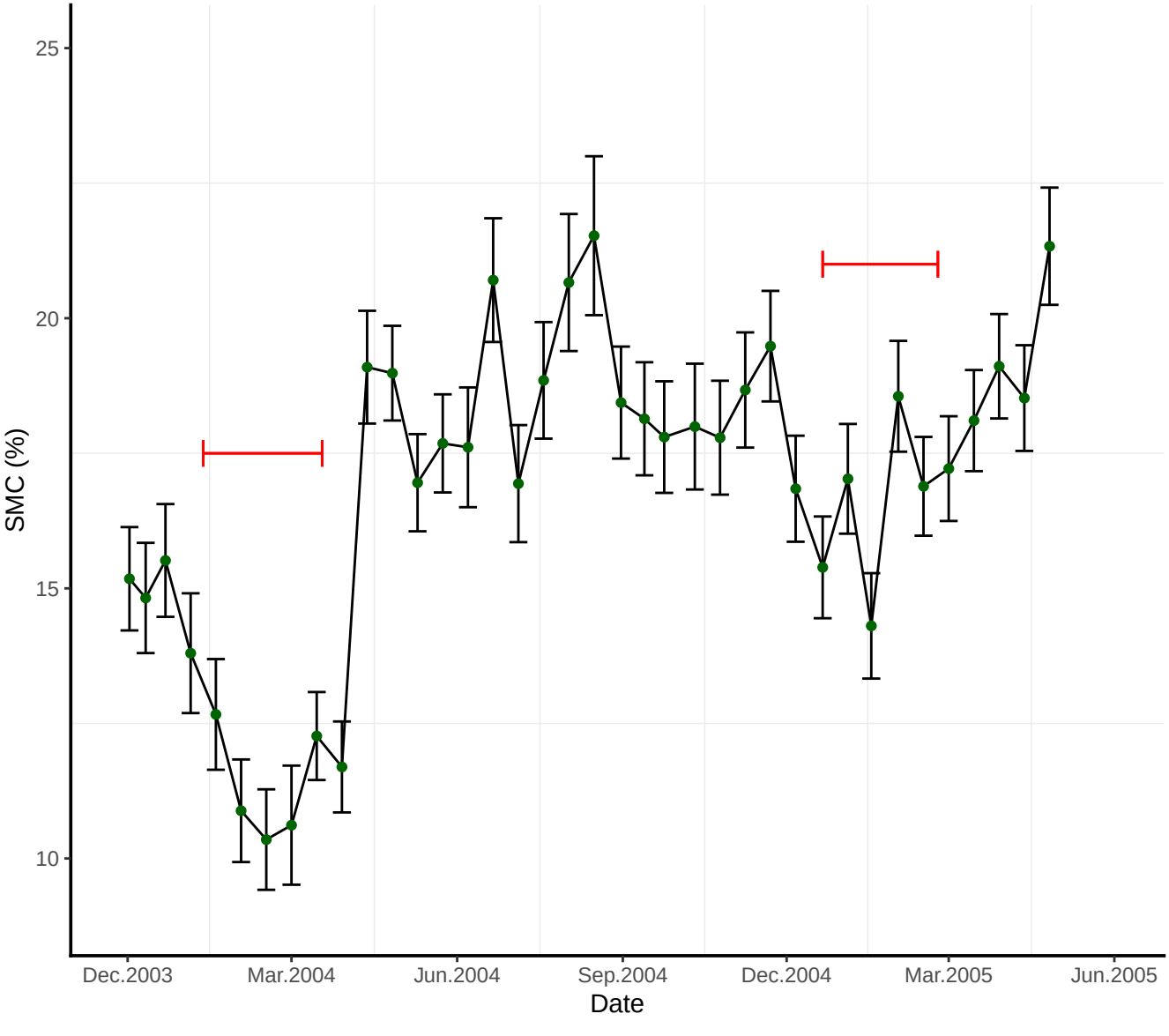
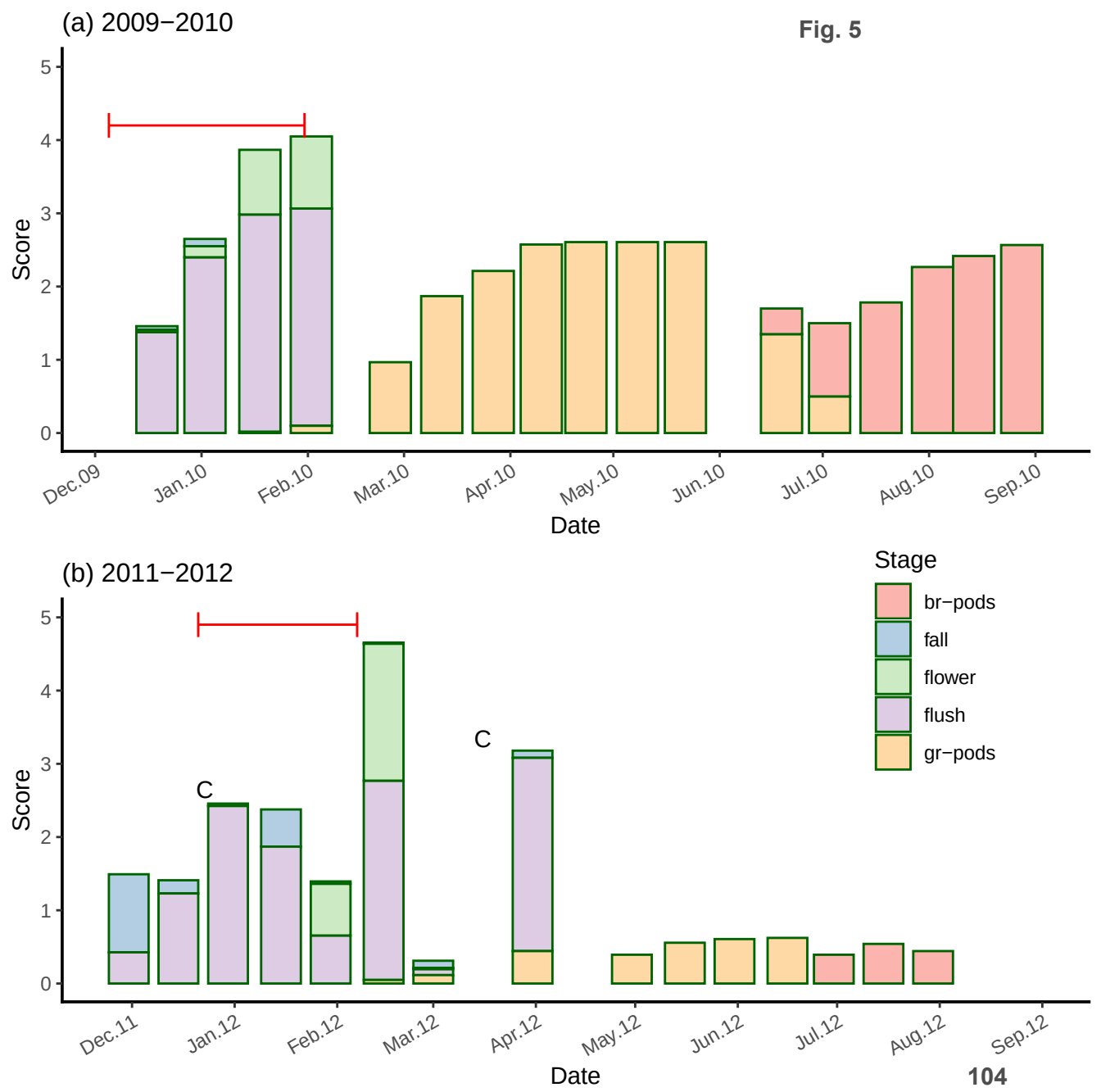

25
20
15
10
SMC (%)
Dec.2003
Mar.2004
Jun.2004
Sep.2004
Dec.2004
Mar.2005
Jun.2005
Date

Fig. 5


(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
Stage
br−pods
fall
flower
flush
gr−pods
Dec.11
Jan.12
Feb.12
Mar.12
Apr.12
May.12
Jun.12
Jul.12
Aug.12
Sep.12

List of Appendices

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