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

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Abstract

Background and aims – The large grove-forming tropical tree *Microberlinia bisulcata* (Fabaceae subfamily Detarioideae) in southern Korup, SW Cameroon, displays strong mast fruiting. The soil is poor in phosphorus and potassium: the climate is strongly seasonal. Evidence is presented that masting is probably determined primarily by mineral nutrients and secondarily by radiation.

Method and materials – Field data on phenology and climate variation (1989 to 2017), and soil moisture, nutrients in litter and fruits, insect herbivory and tree growth are integrated. Some data come from previous studies at Korup, and they are combined with new data to enable an extended analysis.

Key results – To test the nutrient resource limitation hypothesis, phenological recordings were matched with climate variables and modelled using logistic and time-series regressions. A strong predictor was average daily rainfall in the dry season, low in the current year of masting and high in the year prior. Less strong was the increase in dry season radiation between prior and mast years. Masting events showed no relationship to annual stem increment. Masting was reduced after two caterpillar attacks. Fallen-leaf phosphorus concentration increased in the inter-mast interval and that for potassium peaked mid-interval. These elements were likely accumulating and being stored, triggering masting when internal thresholds were crossed. A drier dry season prior to masting may have increased tree carbon, the wetter one increased nutrient acquisition and uptake via roots and mycorrhizas. A rooting–fruiting trade-off in carbon is proposed. Storage of phosphorus may be mostly in bark of branches; that for potassium on soil organic colloids.

Conclusion – The long-term driver appears to be stochastic dry-season rainfall. Synchrony across masting trees might be enhanced by equilibration of nutrients across the mycorrhizal-

root network. Life history strategy determined by mineral nutrient resource dynamics provides the best explanation and an advanced model for the observed pattern of masting events.

Keywords Detarioideae, dry season intensity, ectomycorrhizas, lowland rain forest, mast fruiting, phosphorus limitation, times-series analysis.

INTRODUCTION

By fruiting and seeding intensively at intervals as opposed to continuously over the years, seed and seedling survival may be enhanced for plants species with a masting iteroparous type of life-history as an evolutionary stable strategy (Maynard Smith 1972; Charlesworth 1980; Stearns 1992). Trees provide by far the majority of the documented cases. To explain how a species' fitness can be maintained or increased, a so-called 'economy of scale' concept has often been invoked (Norton and Kelly 1988). Three general processes have been proposed to achieve this type of economy, usually thought of, teleonomically, as the ultimate causes of mast fruiting and seeding: (1) the efficacy of pollination may be increased by mass flowering, (2) seed predators may be more readily satiated by mass seeding, and (3) the chances of successful dispersal and establishment may be improved by larger reproductive output (Kelly 1994; Kelly and Sork 2002; Crone and Rapp 2014; Pearse et al. 2016). Much of the reported research into masting, however, has been in the ecological and evolutionary direction with a strong temperate-biome bias (see reviews aforementioned). Surprisingly, there have been comparatively few studies on masting in the tropics (e.g., Henkel et al. 2005; Ichie et al. 2005a; Newbery et al. 2006a; Norden et al. 2007).

A much more critical issue for understanding masting in trees is the present lack of evidence for, and hypotheses about, the physiological mechanisms which *enable* mast

fruiting and seeding, for both temperate and tropical ecosystems. These mechanisms are commonly viewed by ecologists as being proximate causes. Recent discussions about whether a strict distinction exists between ultimate and proximate causes (Laland et al. 2011; Corning 2019) leave it more open that factors, such as nutrient supply, directly affecting physiological processes might also qualify as ultimate causes of mast fruiting (Fernandez-Martinez et al. 2019; Fernandez-Martinez et al. 2020), although it has been contested whether they can constitute an 'economy of scale' (Kelly 2020).

For flower, fruit and seed production to be allocated efficiently over the life-time of the adult tree as masting years, a set of physiological resource-mechanisms, probably in serial form, must be in place (Lloyd 1980). Resource 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 neighbouring individuals (Yamauchi 1996; Satake and Bjornstad 2008; Abe et al. 2016; Venner et al. 2016; Ye and Sakai 2016; Vacchiano et al. 2018). They have often involved the Moran effect whereby masting is synchronized over large distances by driving climate factors. The triggering is thought to be brought about by a resource level being crossed in the plant which affects plant hormone concentrations that then cue a leafing axil to change to a flowering one, and finally enable fruit maturation (see e.g., Marshall and Grace 1992). In this respect, an individual tree can be modeled as an integrated and dynamic system which controls the timing and intensity of reproductive allocation to masting. Details of the involved physiological mechanisms can be expected to differ across tree species and sites, each achieving a stable yet flexible masting strategy in a different way.

The evidence for C as the main resource directly involved in masting is, however, quite weak. This conclusion comes from direct measurements on whole trees and observations of allocation and experimental manipulation of branches; and from overall C

budgets and studies on the dynamics of non-structural carbohydrates (NSCs) (Hoch et al. 2003; Hoch 2005; Wurth et al. 2005; Millard et al. 2007; Mund et al. 2010; Bustan et al. 2011; Sanchez-Humanes et al. 2011; Ichie et al. 2013; Miyazaki 2013; Richardson et al. 2013; Igarashi et al. 2019; Mund et al. 2020). A few studies have suggested that mineral nutrients may be the key resources underlying budget mechanisms, but the evidence remains scarce because the topic has been so little researched (Bogdziewicz et al. 2024). So far, Han et al. (2014) and Han and Kabeya (2017) have shown that nitrogen (N) storage and mobilization is important for triggering flowering in *Fagus*. Fernandez-Martinez et al. (2017b) and Le Roncé et al. (2023) have indicated that phosphorus (P) and zinc (Zn), and N and Zn, respectively are likely involved in mast fruiting of temperate trees more widely. Carbon should not be laid aside completely as a co-resource though. It is needed with N, P, potassium (K), and other macronutrients, not just to build fruits and seeds, but also indirectly to support growth and maintenance of organs such as fine roots and mycorrhizas which are essential for nutrient acquisition.

If macronutrients do underpin the mechanisms of mast fruiting, it could be expected that the element most important in controlling reproduction might be the one which is at the lowest level of availability at the site relative to the others, that is the one that is in most critical supply overall for the trees (Allen et al. 2017; Fernandez-Martinez et al. 2019). This element will need to be accumulated to support successful reproduction, because seed filling depends on minimally attaining the necessary stoichiometric ratios for all elements required and doing so without undue costs to other tree growth and maintenance demands in the short to medium term. Further, extra-stoichiometric requirements may need to be met where the same element's availability is very low in the soil: a rise in elemental concentration in the seeds would likely be advantageous for seedling establishment.

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

Artificial selection of trees for fruiting under controlled nursery conditions has provided a major insight into tree physiology with regard to fruiting and what may lie as the basis to masting (Davis 1957; Monselise and Goldschmidt 1982; Crawley and Long 1995; Garcia et al. 2021). Cultivated trees often follow an 'alternating bearing' fruiting schedule, with years of 'on' and 'off' harvests over a regular 2-year period. Several temperate tree species in the Fagaceae show such an alternating pattern in natural forest, which leads to the idea that, theoretically, the minimal-intrinsic model across all masting species is perhaps alternating years of reproduction (Newbery et al. 2006a), but in naturally non-fertilized situations the interval between fruiting becomes extended beyond 1 year to allow time to accumulate critical resources and thus allow masting to effect maximize fitness. ('Interval' is here defined as the years of non-masting between masting events.) The fundamental question then becomes, how is the tree system coordinated to synchronize mast fruiting? Nutrient cycles have been strongly implicated in several fruit tree studies (e.g. Rosecrance et al. 1996, 1998).

The main hypothesis of the present paper is that limiting mineral nutrients can determine mast fruiting at the mechanistic, tree-physiological and proximate/ultimate level, particularly for those species that are ectomycorrhizal. This limitation is expected to be

141 strongest where soil mineral nutrients at a site are in critically low supply and
142 ectomycorrhizas are essential to nutrient uptake. Both the tropical Fabaceae subfamily
143 Detarioideae and the Dipterocarpaceae are often ectomycorrhizal (Alexander 1989a;
144 Alexander 1989b; Brearley 2012) and both commonly do show mast fruiting. Among the
145 temperate families (Fagaceae and Pinaceae especially) there is also a strong association
146 between masting and having this symbiotic mode of nutrient uptake (Newbery 2005). Apart
147 from the review of Corrales et al. (2018), the potential role of ectomycorrhizas in masting
148 appears to have largely gone uncommented (e.g. Pearse et al. 2016).

149 Two associated processes could potentially underpin how mast fruiting might be
150 controlled by mineral nutrient limitation. They are not fully exclusive to one another. (i)
151 Ectomycorrhizas might achieve a form of economy of scale due to their putatively extensive
152 shared hyphal networks between the roots of large adult trees (Simard et al. 1997), possibly
153 also via root grafts in dense stands (Graham and Bormann 1966), which could equilibrate
154 levels of the limiting nutrient resource (Newbery et al. 1998), and thereby lead to trees
155 reaching similar internal thresholds simultaneously. (ii) Year-to-year stochasticity in climate
156 (Kerkhoff 2004; Crone and Rapp 2014), especially seasonally-related rainfall, might cause
157 soil nutrient availability and uptake to increase in the interval years between masting events,
158 thus enabling stores to increase across all trees synchronously. For that no economy of scale
159 per se is necessary. Furthermore, these two processes might interact positively, entraining
160 common years of masting because they both depend on ectomycorrhizas and rooting activity.

161 An ecosystem well suited for testing the nutrient resource limitation hypothesis would
162 be high-stature primary forest, for which C is in abundant supply, on soils very low in one or
163 two elements that are macronutrients. Such an opportunity was provided by our long-term
164 work at Korup National Park (SW Cameroon) since the 1970's. In testing the main mineral
165 nutrient hypothesis, it is also necessary to simultaneously test the most likely alternative,

which is that C limitation, driven by radiation levels, determines mast fruiting. This latter aim is supported by an analysis of fruit production in a nearby oil-palm plantation, and a new analysis of previously collected tree ring growth data in relation to masting. Supporting knowledge of tree growth, forest dynamics, nutrient cycling, soils and climate variation at Korup are laid out in the following Background section. This information is essential for fully understanding the framework of the hypotheses being tested and the importance of the two associated processes.

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). For the parts concerning nutrients, some previously published values (as cited) are brought in with the newly reported ones to allow a complete five-element masting interval analysis. In Methods and Materials, and in Results, old and new values are clearly distinguished from one another. In the Discussion section, a synthesis of the new updated results, an improved main hypothesis and schematic model are developed and integrated with a review of the literature. These form a strong basis for new predictions, tests and analyses of mast fruiting in the African detarioids.

BACKGROUND

Forest ecosystem

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). Local and regional maps are found in Gartlan et al. (1986) and Newbery et al. (1988): further details of the site are given in Newbery and Gartlan (1996), Newbery et al. (2006a) and Newbery et al. (2013).

190 *Microberlinia bisulcata* dominates large patches or 'groves', 1–3 km across, in the
191 primary rain forest of southern Korup. Trees ≥ 50 cm stem diameter composed 17.8% of the
192 overall density and 32.6% of total basal area in 2005, and together with co-dominants
193 *Tetraberlinia bisulcata* and *T. korupensis* correspondingly 46.5% and 61.3% (Newbery et al.
194 2004; Newbery et al. 2013). All three species are strongly ectomycorrhizal as are several
195 other co-occurring tree species of the subfamily Detarioideae in the Fabaceae, (formerly
196 Caesalpiniaceae-Leguminosae, Newbery et al. 1988). The taxonomy follows the revision of
197 LPWG (2017) and de la Estrella et al. (2018). They are not N-fixing trees. *Microberlinia*
198 *bisulcata* trees attain considerable stature in the main canopy, characterized by wide dome-
199 shaped crowns, and very extensive laterally spreading buttress systems (Newbery et al. 2009;
200 Newbery et al. 2013). The species is a leaf-exchanger and therefore semi-deciduous: new
201 leaves at the start of the dry season (December to February) push off the old leaves, flowering
202 follows within a month (Newbery et al. 1998; Newbery et al. 2006a). Flowers are outcrossed
203 mainly by small bees and pollen seems unlikely to be limiting: bees are highly abundant in
204 the canopy during the dry season (Newbery et al. 1998). It remains untested, however,
205 whether insect pollination could form an economy-of-scale factor: in this connection
206 presumably the density of trees plays a crucial role. Into the wet season (March to October)
207 pods mature from soft green to hard fibrous brown structures. Seeds are dispersed
208 ballistically in August-September (Norghauer and Newbery 2015).

209 The Korup-Ndian area along with Douala at the coast is climatologically special for
210 western Central Africa because it has one clear dry season each year as opposed to the two
211 less-distinct ones found elsewhere in the region. Mean annual rainfall for 1984–2016 was
212 5159 mm (range 4023 to 6531 mm). The typical seasonal course in rainfall is shown in
213 Newbery et al. (Newbery et al. 1997), with almost none in January and February but reaching
214 900–1000 mm in August or September. Site elevation of the site in southern Korup National

215 Park (KNP) is ~120 m a.s.l. (range of 40 to 200 m from south to north inland), slightly
216 varying between swampy stream-fed lower areas up to local slopes, in places strewn with
217 quartzite rocks. The soils are very sandy and free-draining, acidic and very low in available P
218 and K (Gartlan et al. 1986), meaning that here high-stature tropical forest is growing on one
219 of the most nutrient-poor sites in tropical Africa. Within groves at Korup, soil organic matter
220 is largely confined to the top 2 cm of the profile, forming a surface mat that is densely
221 occupied by fine roots and ectomycorrhizal hyphae (Newbery et al. 1988; Newbery et al.
222 1997). Larger vertical roots can tap deeper water reserves. Nutrient cycling in the groves
223 shows a 'fast-forward' modus: leaf litter decay is fast, there is no permanent leaf litter layer,
224 and most cycling via the very efficient mat happens in the early wet season (Chuyong et al.
225 2000, 2002). At this time throughfall nutrients help to prime decomposition and uptake
226 (Chuyong et al. 2004). For the rest of the year, heavy rains leach the forest, and this results in
227 a tight closed ecosystem in which ectomycorrhizas play a central role in P acquisition and
228 uptake (Newbery et al. 1997). In addition, during each year's dry season, Harmattan dust
229 brings some P to the forest via aerial deposition. A critical field experiment showed that
230 growth and recruitment of *M. bisulcata* is not P-limited (Newbery et al. 2002), possibly
231 because of its highly evolved adaptations to the low P site or another element like K was
232 limiting.

233 Recruitment of *M. bisulcata* over at least the last six decades has been poor due to
234 very low seedling and sapling survival (Newbery et al. 1998; Newbery et al. 2000; Newbery
235 et al. 2006b; Newbery et al. 2010; Norghauer and Newbery 2010). Seed production in mast
236 years is copious (Newbery et al. 2006a) but this species' seedlings are shade-intolerant
237 (Green and Newbery 2001a, 2001b). The groves demonstrate transient dominance: the stands
238 now are predominantly made up of large to very large trees, with extremely few small ones
239 present (Newbery et al. 2013). The dynamics is thought to be one of patches arising and then

240 decaying, being replaced, *in situ* or *ex situ*, within a mosaic of species-richer forest (Newbery
241 and Gartlan 1996; Newbery et al. 2013). The species is classified as a long-lived light-
242 demanding tree (see Newbery et al. 2010). Part of the expected life-history strategy of long-
243 lived and light responsive species such as *M. bisulcata* would be to delay size at the onset of
244 maturity (SOM) in order that greater seed output later offsets the relatively low probability of
245 persistence in the forest understorey. Two further coevolved traits are the ectomycorrhizal
246 habit mentioned and mast fruiting. Ectomycorrhizas not only provide advantages in resource
247 acquisition for juvenile and young adult trees but are also thought to be a means to store
248 resources which enable mast fruiting in the older adult ones (Newbery et al. 1998; Newbery
249 et al. 2006a). A key sub-hypothesis has been that these links between adults synchronize the
250 timing of masts by equilibrating nutrient sinks across groves (Newbery et al. 1997; Newbery
251 et al. 1998). There is mounting evidence from other forests that ectomycorrhizas build
252 intricate below-ground hyphal networks between individual trees (e.g. Simard and Durall
253 2004; Simard et al. 2012), although the definite evidence for these networks providing a
254 means of C or mineral nutrient transfer is inconsistent, at least for adults to seedlings (Karst
255 et al. 2023). However, in the context of mast fruiting of adults, the hypothesized transfers are
256 between very large trees occurring in dense stands (the groves at Korup).

257 **Mast fruiting**

258 Mast fruiting in *M. bisulcata* was first realized from early phenological recording in
259 1988 to 1995, with prominent seed crops in 1989, 1992 and 1995 yet barely any seed fall in
260 the intervening years (Newbery et al. 1998). Flowering occurs to some extent in most years (a
261 few fail completely); though not always does a heavy seed crop depend on heavy flowering
262 (Newbery et al. 2006a). The two *Tetraberlinia* species tend to mast in the same years as *M.*
263 *bisulcata* but not both together (Newbery et al. 1998, and unpublished data). After a
264 propitious start with a potential 3-year cycle for masting (i.e. a 2-year interval between mast

265 years), this cycle turned out to be shorter between 1999 and 2005. Because masting was
266 associated with peaks in mean daily radiation in the dry season prior to fruiting this suggested
267 that C was at a premium, with some threshold needed to be crossed before masting occurred.
268 Detailed nutrient cycling studies in plots dominated by *M. bisulcata* showed, for the first
269 time, that leaf litter falling after masting in 1989 was low in P concentration compared with
270 the dry season of the years before and after (1988, 1990) , and this matched a decline in
271 available P in the soil, especially in the surface organic layer (Newbery et al. 1997). This last
272 result suggested that P was being shunted into the seed crop and less was remaining to be
273 shed in litter and, given the low soil P at the site and the presence of ectomycorrhizas, P was
274 also likely limiting mast fruiting. Tree C and P levels might be operating a double-threshold
275 control system and this led to the phosphorus and climate proposed ectomycorrhizal response
276 (PACER) hypothesis (Newbery et al. 1997).

277 The climate at Korup varies stochastically from year to year, particularly regarding
278 the start, duration and intensity of the dry season. The dates defining the actual season each
279 year are based on 30-day running rainfall total (*rft*) falling < 100 mm (Newbery et al. 2006a).
280 This season plus the first 6 weeks of the wet season very largely determine tree physiological
281 processes for the whole year. Fine-tuned sensing of the environment to optimize resource
282 gain and allocation within a life history strategy is central to survival. Under- or over-
283 allocation at the wrong time could lead to large fitness losses, hence the presumed operation
284 of thresholds that safely trigger phenological change. That C and P might be dual constraints
285 within a broader nutrient-limitation hypothesis as an explanation of mast fruiting for many
286 tree species requires a detailed budget to determine how much C and P (also N and K) are
287 allocated to fruits and seeds in a main masting event. Censuses of seed and pod counts, along
288 with their masses and nutrient amounts, were obtained for the 1995 masting (Green and
289 Newbery 2002), showing that *M. bisulcata* produced on average 26K seeds per tree or 83.5K

seeds/ha. Seeds are small (0.64 g each), and with an average of 2.0 seeds per pod, total pod mass was 25 g (see images in the Suppl. material of Norghauer and Newbery (2015); for the 2007 and 2010 events, 2.5 seeds per pod were estimated. Masting resulted in an investment of 1034 kg /ha dry mass that year, and compared with leaf litter production in previous non-mast years (Chuyong et al. 2000), was 52% of it by comparison, or in a mast year 74%, i.e. a substantial allocation of resources (Green and Newbery 2002). Seeds and pods together had N and P amounts 13 and 21% of that in annual leaf litter production, indicating 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. Masting in *M. bisulcata* is highly synchronous, and it is unusual for a spatially isolated tree to fruit outside of an event (Newbery et al. 1998; Newbery et al. 2006a).

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 *drier* than average (more intense, low mean daily rainfall), plus the dry season in the year prior was *wetter* than average (less intense, high mean daily rainfall). After 1993, radiation did not show the same trend as in 1989–1992, mainly because after 1995 it climbed steeply as part of an inferred 11-year solar cycle (Newbery et al. 2006a). The relative change in radiation between successive years was important, and not the absolute levels. The notion that time series of relevant environmental variables at Korup were or ever had been stationary is hard to sustain.

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

METHODS AND MATERIALS

Climate records

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 Jan. 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 (Suppl. material 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 the analysis in Suppl. material 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 time series referenced in Suppl. material 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 and the special topography around Mt. Cameroon (SSE of Korup), with the few data records available for the last decades being incomplete (see Suppl. material 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 often being shorter or longer. Hence, in what follows, 'dry season 1991' for example means December 1990 to February 1991 (modally). For a more general, less strict, annual matching of phenology to climate, a 12-month year starting on 1 December one year and ending on 30 November the next was adopted, with quarter 1 being December to

363 February, and so on. Part-years were taken as November to March (5 months, dry) versus
364 April to October (7 months, wet) to encompass the weeks before and after the dry season
365 proper. Since its use in Newbery et al. (2006a), the definition of drought dry season was
366 slightly relaxed here, in that within the outer defining limits a very few days where *rft* was at
367 < 103 mm were included as drought days provided that the total returned to below 100 mm
368 for the rest of the season. This affected four of the 16 years slightly in their dry season
369 durations and mean daily rainfall values (Table 1).

370 **Phenological recording**

371 The main 'P-plot' is located in the southern part of the Park (5º10' N, 8º70' E; global
372 coordinates 0476438/ 0553538) at an elevation of 96 m a.s.l.: refer to Newbery et al. (2004)
373 and Newbery et al. (2013) for further details. Mast fruiting from 1989 to 2004 was reported
374 and analysed in Newbery et al. (2006a). Recordings were then continued from 2005 to 2017
375 for a subset of trees, and it is this full time series of 29 yr that is presented, with an extended
376 analysis, in the paper here. Following pod maturity to completion was not possible in 2017
377 because of security restrictions preventing further access to KNP. The situation remains
378 unresolved as of early 2025.

379 Evidence for masting rested on a combination of intensive phenological scoring of
380 marked trees in two periods, quantitative trap-based estimates of seeding in two specific
381 studies, from which masting fruiting is inferred; circumstantial records linked to seedling
382 demography and seedling experiments in several years, and general yet objective assessments
383 of the whole forest in other years during the course of large-plot census work, dendroband
384 recording times, and seedling herbivore exclusion and nutrient lysimeter studies. (Suppl.
385 material 2, table 1). Barely a year passed without adequate observation and reporting because

386 of the continuing project workflow and frequent field presence of the Stirling-Bern research
387 group since 1988.

388 The two periods of intensive recording were achieved in the following manner. To
389 increase the frequency of recording per annum between 1995 and 2000, 150 *M. bisulcata*
390 trees in the main 82.5 ha 'P-plot' (out of 294 in total with stem diameter ≥ 50 cm; Newbery et
391 al. 2013) had been scored on 61 occasions (mostly at monthly intervals), for intensity of leaf
392 fall, leaf flush, flowering and immature and mature pods: scale 0, none; 1, ~25; 2, ~50; and 3,
393 ~75 and up to 100% (Newbery et al. 2006a). Later, within an 8-ha sub-area of the 82.5-ha P-
394 plot (1000–1200 m E, and 100–500 N, with respect to SW origin; see Fig. 2a of Newbery et
395 al. (2013), 61 of the 65 trees surviving since the last enumeration in 2005 (stem diameter,
396 mean ± SE = 112 ± 4 cm, range = 54–174 cm), were scored between 2009 and 2013 in a
397 similar manner as the first period. In 2014, fallen pod density on the ground was taken as a
398 proxy for mature pod density (Suppl. material 2, table 1).

399 Masting was categorized as 'high' (labelled 'M') when all, or almost all (> ~85%), of
400 the recorded trees had many pods (scale = c. 3), and 'moderate' ('m') when fewer trees (~45–
401 85%) had many pods, or numbers of pods on relatively more trees were significantly lower.
402 These masting events were clearly differentiated from those with 'no' or 'very low' pod
403 production, and from those 'low' ones with just a few to several (~ < 20%) trees masting
404 (Suppl. material 2, table 1: the Evidence Table). The masting scale was therefore semi-
405 parametric: except for the last 2 years the scale was quasi-binomial. In the Results section,
406 three categories of event are use: 'M' and 'm' as masting; and the set "none, very low and
407 low" as non-masting. Direct estimates of seed output, as a quantitative measure of mast
408 fruiting, or even qualitative crown scoring, for all trees in all years was simply not feasible at
409 this remote and difficult field location. The reduced and simplified scale for masting provides

410 the best lowest denominator allowing all years of recording to be combined with very little
411 bias.

412 Two canopy caterpillar outbreaks in 2011-12 and 2014 offered the opportunity to
413 assess how loss of foliage to herbivory, and hence photosynthetic activity, could have
414 interfered with tree reproduction.

415 **Nutrient sampling**

416 *Previous litter samples providing inter-mast nutrient data*

417 In an earlier-conducted litterfall study between May 1990 and June 1992, monthly
418 bulked samples from twenty 40-cm x 40-cm traps in each of 10 subplots had been divided
419 into two halves: as set A, for separation into fractions (leaves, small wood, etc.), and set B,
420 for separation of just leaves into the commonest 26 species (Chuyong et al. 2000). From this
421 set B, leaves of *M. bisulcata* were selected and later – as for the other species – they are
422 analyzed for N, P, Ca, K and Mg concentrations. Leaflets and rachises were kept together. As
423 this species is a leaf-exchanger, it has a very well-defined period of leaf litterfall each year,
424 starting with onset of the dry season (Newbery et al. 2006a). Five subplots were in low
425 (LEM) and five in high (HEM) ectomycorrhizal stands (each 40 x 80 m) along the transect P
426 in Korup (Gartlan et al. 1986; Newbery et al. 1997). Since *M. bisulcata* occurred in only the
427 HEM subplots, the number of replicate nutrient values per month was five. The 26 months
428 had been divided into seasons according to the median rainfall pattern at Korup (as defined
429 above), with those in the dry season being generally December 1990–February 1991 and
430 December 1991–February 1992, and the other months the longer wet seasons. Only dry
431 seasons are considered here, and nutrient concentrations for them are now averaged across
432 the three constituent months. A mast fruiting occurred in (August-September) 1989, so dry
433 season 1990–1991 is the second dry season after the event, and dry season 1991–1992 the

434 third one. The next masting was in the wet season of 1992, so seen from this perspective the
435 two dry seasons selected were ~ 6 and 18 months prior to the second event.

436 In a later unpublished study of litterfall by Schwan (2003), paired litter traps (same as
437 those used by Chuyong et al. 2000) were placed at random below the crowns of 20 *M.*
438 *bisulcata* trees in the main P-plot. The bulk of the litter (~90%) fell in the 3-week period of 9-
439 30 Dec. 2002. This 2002–2003 dry season came immediately after a masting in 2002, and
440 next one was in 2004 (Newbery et al. 2006a). In this study by Schwan (2003) only leaflets
441 were analyzed for N, P, K and Mg.

442 *New litter samples included in the inter-mast data set*

443 In the dry season 1997–1998 four traps of galvanized metal (same as used in 1990–
444 1992) were compared with four similar ones but lined with hessian sacking (used in the
445 1989–1991 study of Newbery et al. (1997), each set being placed at random in each of the
446 two quarter plots of six HEM half-plots. Litter was collected over four consecutive fortnights
447 between 21 Dec. 1997 to 15 Feb. 1998. *Microberlinia bisulcata* leaflets and rachises were
448 again sampled separately, dried and analyzed for N and P concentrations. Not all traps had
449 sufficient material and the replication per subplot/trap type/date ranged from 2 to 4. The N
450 and P values were successively averaged for trap type, then subplot, and their weighted 4:1
451 leaflet-rachis averages found for the 24 date x plot combinations. Trap type had no effect on
452 these two elements' litter concentrations (initially to test for Zn contamination). This litterfall
453 was collected midway between a moderate double masting in wet seasons 1997 and 1998.
454 Chemical analysis followed Chuyong et al. (2000).

455 An opportunity to sample *M. bisulcata* leaf litter immediately after a later mast
456 fruiting came in the 2010–2011 dry season. A large system of over 400 seed traps had been
457 used to follow seed production and dispersal in the August-September 2010 masting

(Norghauer and Newbery 2015). These traps remained in place until early 2011, collecting leaf litter. The dry season started on 26 Dec. 2010, and samples were taken on 29 Jan. 2011. This interval of ~1 month would have covered a very large proportion of the leaf fall of this species that year, although the thin tail into February was not included. Thirty traps, from 68 small clusters of the traps within 25 ha of the 82.5-ha permanent plot Newbery et al. (2013), had sufficient quantities of almost-only *M. bisulcata* leaves, lying in the traps as a well-defined readily collectable upper layer. Leaflets and rachises were separated on this occasion and analyzed for the same five elements as in 1990–1992, later recombining at the whole leaf level. The mean dry mass ratio of leaflets to rachis in *M. bisulcata* leaves was 0.793:0.207, very close to a 4-to-1 ratio.

Nutrients in seeds and pods: extending the earlier data set

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, leaf litterfall values from 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 very slightly underestimated mature leaf mass because of 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.

Soil moisture measurement

481 Soil moisture was recorded across two dry seasons to demonstrate that its variation
482 could underpin soil nutrient processes which were affecting mast fruiting. *Microberlinia*
483 *bisulcata* trees spread their extensive lateral fine root systems and ectomycorrhizas mainly in
484 that drying soil surface layer (Newbery et al. 1997; Newbery et al. 2009). An additional aim
485 was to determine by how much soil moisture content was reduced by rainfall deficit.

486 On 2 Dec. 2003, 12 soil moisture content sensors (Theta Probes ML2, Delta-T
487 Devices, Cambridge, UK) were installed in a stratified random manner across the eastern 30
488 ha of the P-plot, one per block of 100 m x 250 m. Each probe was inserted horizontally (at 40
489 cm depth, excepting three at 20 cm due to access problems) into a hole excavated at the side
490 of a small pit, the latter backfilled and packed down to the original density. A subsample of
491 soil from the excavated side hole was retained to measure its fresh, water-saturated, and later
492 oven-dry weight (105 ^{o}C). With a hand-held meter, soil moisture content (SMC, %) was
493 recorded fortnightly until 26 Apr. 2005 (38 times). Readings were repeated between 15 Nov.
494 2006 and 15 Mar. 2007 (nine times), with one last recording on 29 Jan. 2011. In the years
495 2004 and 2007 *M. bisulcata* had major mast fruiting, in 2005 and 2011 it had none.

496 **Statistical analysis**

497 The fitting of masting, as a 0/1 binomial response variable, to the climate variables
498 was first limited to the 24-year period 1989–2012 because all the events were strong and
499 pronounced ('M' in Table 1; Suppl. material 2, table 1). Logistic regressions were run with
500 dispersion (φ) either fixed at 1.0 or estimated (Agresti 2007). Whilst the latter gave
501 marginally more significant fits, the former was adopted because the sample size was small
502 and the estimation of φ would be unreliable (McCullagh and Nelder 1989). The binomial
503 error distribution appeared to be satisfactory: the complementary log-log one did not improve
504 fitting. Simple logistic regression does not account for temporal autocorrelation, however.

With records for only ~60 trees in common across all events, the sample size was too small to apply Monte Carlo subsampling in order to achieve temporal independence. Because of the non-stationarity, randomization tests will not provide valid inferences (Cox 1981).

Extending the analysis to the full 29 years (1989–2017) required the ordinal, or proportional-odds, logistic model (Agresti 2007; Fox 2008; Hosmer et al. 2013), where 'm' (moderate masting) was scored as 0.5 (see Suppl. material 2, table 1). Binomial and ordinal logistic models were run with the 'glm' and 'polr' commands in R (Venables and Ripley 2002; Fox and Weisberg 2011), using the 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. Because mean daily dry season rainfall and radiation were not correlated, these variables were fitted in separate models (see Results).

Times-series logistic regression – in full, generalized logistic autoregressive moving-average regression, with the command 'glarma' (R package glarma, Dunsmuir and Scott 2015) – accounts for temporal autocorrelations in binomial data (Cox 1958, 1981; McKenzie 1985; Cox and Snell 1989; McKenzie 2003; Dunsmuir 2016) and it was applied to the masting data.

RESULTS

Mast fruiting pattern

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

Climate variation in time

Of the four basic climate variables, mean rainfall and radiation per day in the dry season along with the start and length of the season (current year of masting and year prior), only the first required ln-transformation to remove positive skew along the independent variable axis. Dry season rainfall and radiation were not significantly correlated ($r = 0.110$, $P = 0.57$, df = 27) and could be treated as being independent.

Mean daily dry-season rainfall in years of full masting was lower than in those years' prior with no masting (Fig. 2a) except for 2000. Further, 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 (Suppl. material 3, fig. 3) 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

552 included the lagged 1988-value.) Radiation over time showed a distinctive pattern with a
553 clear central peak between 1996 and 2005, then a rise again, apart from 2009, to those higher
554 levels (Fig. 2b): accordingly, the series evidenced non-stationarity, and as a consequence
555 autocorrelation was positive and significant for lags of 1 and 2 years, then significantly
556 negative ($P < 0.05$) for lags of 6–8 years (Suppl. material 3, fig. 3). The partial
557 autocorrelation remained significant for a lag of 1 year only, however.

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

572 **Modelling masting and climate**

573 Binomial logistic regressions for 1989–2012 showed a significant negative effect of
574 mean daily rainfall in the current year's dry season ($P < 0.05$), and a positive effect of mean
575 daily rainfall in the dry season prior ($P < 0.05$), on masting. Using ln(*rain*) and ln($rain_{-1}$)

improved the regressions fits with $P < 0.015$ (Suppl. material 4, table 1). Mean daily rainfall was only weakly correlated with rainfall the year prior: untransformed values ($r = –0.190$, $P = 0.374$), transformed ($r = –0.272$, $P = 0.15$). This last result is important because a strong negative temporal autocorrelation, i.e. a year-to-year increase-decrease reversal, was absent. Regressions with both rainfall terms led to reduced fitting, because these coefficients were now partial ones adjusting for the correlation ($P = 0.093$ and 0.055). The same regressions with ln-transformed variables also changed the significance levels very little ($P < 0.10$; Suppl. material 4, table 1). 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 ($P < 0.01$), having coefficients with the same signs as for the binomial logistic ones (Suppl. material 4, table 1) and, whilst significance decreased again using two-term models, the fits were still relatively strongly significant overall ($P < 0.025$).

The mean difference in ln-transformed dry-season mean daily rainfall, ln(*rain*), between the current masting (t_0) and year prior ($t_{–1}$) was highly significant ($P < 0.005$), but much weaker for the same and penultimate year ($t_{–2}$) ($P = 0.15$). Back-transformed means were 1.37, 2.49 and 1.69 mm/day respectively (see Suppl. material 4, table 2). Comparing rain at t_0 with means of *rain* at $t_{–1}$ and $t_{–2}$ – applying equal or unequal weighting – led to very similar results as those at $t_{–1}$ alone ($P < 0.005$). As a robustness test of the strong vs moderate ('M'/'m')-grading of mast fruiting, and how that might have affected the relationship with mean daily rainfall in the dry season where there was some uncertainty in the final grading, the 1989–2017 ordinal logistic regressions were rerun with '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, for 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 (Suppl. material 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). Hence there was 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 did show a long-term trend from the start of recording until 2017 (Suppl. material 3, fig. 2), with evidence of a 11-year solar cycle. This was not related to the change in instrumentation at Bulu (Suppl. material 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 (Suppl. material 3, fig. 2[a]). 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).

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

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

Predicting masting from models

Using binomial logistic regressions of masting 1989–2004 on ln(*rain*) in the current and previous years, fitted models were used to predict masting in 2005–2017 (Fig. 1), on the original response scale of 0 to 1 (π; Agresti 2007). The series started at 1989, not 1987 as used in Newbery et al. (2006a); and autocorrelation was not incorporated (see 'Time series analysis' later though). The model fit for ln(*rain*) was good for the mast years 1989, 1992, 1995 and 1997 (marginal for 1998), and good for 2002 and 2004, but it wrongly indicated a mast in 1993 and missed the mast in 2000 (Fig. 1b; fitted intercept [α] = 3.61 ± 1.80 and slope [β] = –5.77 ± 2.62, $t = -2.206$, $P = 0.027$). Predictions of masting in 2007 and 2010

were very high (π = 0.97 and 0.83 respectively), and also that it did not occur in the intervening years. After 2012 though, one each of the pairs of moderate ('m') masts was predicted as full ('M', π = 0.98 and 0.97). The predicted masting in 2005 (π = 0.75) was incorrect, however.

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

The median effective level of ln(*rain*), that is the level when π (x) = 0.5 (defined as x = $-\alpha/\beta$; Agresti 2007) was 0.624, which back-transformed to 1.869 mm/day – a value very close to the estimate for the ln($rain_{-1}$) estimate of 1.867 mm/day. This median level, which might be interpreted as a form of threshold for non-masting and masting, applied well to the events and their rainfall values in most years up to 2011 (Table 1, Fig. 2a), although ln(*rain*) and ln($rain_{-1}$) differed in a few years as being better or worse fitting and predicted. Years 2012, 2013 and 2014 had moderately high and quite similar mean rainfall in their dry seasons (1.90–2.07 mm/day; Table 1), so aside from the caterpillar intervention, the rain threshold theory would not have been expected to work too well – a form of counterfactual evidence.

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

Time series approach

Application here supported the binomial logistic regression results for 1987–2012 even more strongly ($P < 0.01$ and $P < 0.05$ for ln(*rain*) and ln($rain_{-1}$) respectively, for both lags p = 1 and 2, (Suppl. material 4, table 1). Regressions using the time-series logistic regression model for *radi*, $radi_{-1}$, *start* and $start_{-1}$ either failed to converge or the fits were insignificant ($P = 0.17$ to 0.73). Whilst there was a weak positive effect on masting for duration in the current year ($\beta = 0.041 \pm 0.025$, $z = 1.64$, $P = 0.10$), an even stronger negative effect of duration was evidenced for the year prior ($duration_{-1}$; $\beta = -0.099 \pm 0.038$, $z = -2.62$, $P = 0.0087$) (Suppl. material 4, fig. 2). The last relationship analyzed before with a binomial logistic model was only marginally significant ($P = 0.073$), so the evidence for the effect improved.

The dependence of mast fruiting on dry season rainfall appears to be limited to the current and previous (t_{-1}) years, because repeat runs replacing $rain_{-1}$ with $rain_{-2}$, the mean daily rainfall in the second year prior to the current one (t_{-2}), were all clearly insignificant ($P = 0.39$ and 0.40) for 1989–2012 binomial logistic regressions, rainfall ln-transformed, single and two-term models respectively; and they were correspondingly insignificant ($P = 0.35$ and 0.76) for the 1989–2017 series with ordinal logistic regression. Moreover, dry-season rainfall at t_{-2} was poorly correlated with the same in the current year ($r = 0.027$ and 0.110), but slightly better with that at t_{-1} ($r = -0.187$ and -0.257). Time-series logistic regression fits did not improve fitting to intensity of radiation (current or prior), differences in dry season radiation in successive years, or smoothed radiation regression residuals (current or prior) (*P*

= 0.094, 0.062, 0.25, 0.74 and 0.26; respectively). Finally, masting was unrelated to minimum temperature in the current year's dry season (1989–2012, Table 1; binomial logistic $P = 0.18$; and 1989–2017, ordinal logistic $P = 0.24$).

Extending models for radiation

Whilst a rainfall deficit delimitation will define the drought period in terms of limited water availability, it may not necessarily correspond precisely to times of heightened radiation. Returning to the modal definition of dry season, namely the calendar months December through February (DJF), or first quarter of the phenologically-referenced year, mean daily radiation can likewise be found (Suppl. material 3, fig. 1). 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 ($P \geq 0.18$; Suppl. material 4, table 3[a]), and also not for the other three quarters (Suppl. material 3, fig. 1; $P > 0.4$; 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 the current year, and with all three regression models ($P = 0.007$ to 0.024; Suppl. material 4, table 3[a] and fig. 3; and Suppl. material 3, fig. 1). Using again LOWESS smoothing regressions to remove trend in radiation (Suppl. material 3, fig. 2[b]), with binomial logistic regression (1989–2012) masting weakly positively depended on differences in *radi* ($P = 0.051$) and negatively, though more marginally, for $radi_{-1}$ ($P < 0.1$) (Suppl. material 4, fig. 3 and table 3[b]). Time-series logistic regressions improved the fits especially for *radi* ($P < 0.02$), although only slightly for $radi_{-1}$ ($P = 0.08$). Fits to detrended differences (1989–2017) with ordinal logistic regression were intermediate in significance to those with binomial and time-series logistic ones (Suppl. material 4, table 3[b]). Overall, there emerged moderate to strong evidence that the larger the increase in radiation between successive years, or the more

722 positive the difference from the trend, the more likely a mast fruiting. This difference effect
723 was not obvious in the earlier analyses of Newbery et al. (2006a).

724 An interesting feature of the LOWESS fits (Suppl. material 3, fig. 2), when taking
725 radiation according to the two definitions of dry season, is how the outliers changed in
726 relation to the smoothed curves. In the drought-defined case, 2001 and 2003 (both 1 year
727 before masting) were very high, and 2006 and 2009 (also both 1 year before masting) were
728 very low. Changing to the DJF-defined case brought 2001 and 2009 radiation much closer to
729 the curve, and the binomial and time-series regression fits were improvements. Further, the
730 autocorrelation was notably stronger, positive and significant, at lags of 1 and 2 years for this
731 DJF-defined dry season than the drought-defined one, shifting to a significant negative
732 correlation at an 8-year lag (Suppl. material 3, fig. 4). The partial correlation, again, remained
733 significant for just the lag of 1 year. In the third (JJA) and fourth (SON) quarters a similar but
734 slightly weaker pattern for the function occurred, the negative lag now at 10–12 years (Suppl.
735 material 3, fig. 4). More interesting, however, was the almost unstructured weak pattern of
736 the function for the second (MAM) quarter, which is no temporal autocorrelation over the
737 early wet seasons (Suppl. material 3, fig. 4). Difference in radiation was significant for a lag
738 of 3 years, and remained almost so for the partial correlation, hinting at the 3-year cycle.

739 **Start and duration of the dry season**

740 To shed some light on the apparent paradox of the different definitions of dry season
741 determining the relationship between masting and radiation, regression models were rerun
742 with an extended dry season of the months of November through to March. All binomial
743 logistic model fits, 1989–2012, using radiation in the current and prior dry seasons on this
744 new basis were clearly insignificant (P = 0.27 and 0.69). However, dependence on masting
745 on $radi_d$ was marginally significant at P = 0.071 ($radi_{d\%}$, P = 0.052), and correspondingly so

was it for the time-series logistic model with p = 2 (P = 0.056 and 0.043). Compared with the fits for the models using DJF as dry season (Suppl. material 4, table 2[a]), these results for the 5-month season were weaker, suggesting that the influence of radiation was being diluted by inclusion of the additional 2 months; and this was reflecting the early wet season autocorrelation. Comparing radiation defined by DJF and that defined by the drought dry season graphically, both for differences between successive years and as residuals from the smoother curve over time (Suppl. material 4, fig. 4), 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. This confirmed that raised radiation differences and deviations were associated with mast fruiting.

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

When the mean daily radiation of the non-overlapping weeks with DJF increased or decreased, or vice versa, the $radi_{d\%}$ altered between successive seasons. Since masting fitted to $radi_d$ much better for the DJF- than drought-defined seasons, this would suggest that (a) radiation levels outside of the DJF months were most likely important, and (b) DJF-defined seasons allowed a more consistent year-to-year comparison than the drought-defined ones. That rain may have been lacking, which defined the duration of the drought-defined season, did not also imply radiation was changing proportionally. Radiation could have been sometimes high in the day and rain fell at night: conversely radiation could have been low

when there was cloud cover and yet no rain, as was the case in some years at the transition to the wet season. Differences in successive years' dry season radiation were more, respectively less, pronounced in the first and second halves of the time series, for the DJF- than the drought-defined dry seasons.

Soil moisture content in dry season

On graphing the time series for 2003–2005, three of the 12 sensors had three anomalous and coinciding high peaks (~ 40 - <60%) in the 2004 and 2005 early-to-mid wet seasons suggesting that their locations were prone to flooding. These sensors' data for the whole period were accordingly omitted. Two of them were actually destroyed later by hunters. The time series of mean SMC is shown in Fig. 3: it included the two dry seasons of 2004 and 2005, defined as before as when *rft* fell < 100 mm. Mean SMC over the 1.4 years was 16.80 ± 0.48%. Repeated measures analysis of variance for six times within each of the two dry seasons (Fig. 3), using all 12 sensors' values, indicated that differences in mean SMC at the 20-and 40-cm depths were very small and insignificant: 10.98 vs 10.69% in 2003–2004 and 16.20 vs 15.89% in 2004–2005, $P = 0.88$ 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 2003–2004, during which SMC reached a minimum of 10.4%, its values remained fairly constant at 18.24 ± 0.31%. The dry season of 2004–2005 had much less influence on SMC (Fig. 3). The lowest SMC-values in 2004 coincided with the lowest *rft*-values (down to 12 mm then 0 mm over 4 weeks); in 2005 the SMC either did not go so low or remain low for long, and the match with SMC was weaker. At the start of the

2003–2005 series, the means (± SE) of SMC recorded and those found by gravimetric analysis were 15.09 ± 0.52 and 15.50 ± 0.82% respectively. The estimates were positively correlated (r = 0.677, df = 10, P = 0.016). Saturated water holding capacity was on average 38.15 ± 1.16%, less than the SMC at the peak times, confirming that some locations were not always free draining.

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

The 30-day running rainfall total, *rft*, used to define the dry season in terms of drought when this total goes below 100 mm, does not indicate either how much is the deficit, or how steep is the decline into, or incline out of, the dry season. Suppl. material 5, fig. 1 shows the course of *rft* as the daily rainfall events occurred. The intense dry season of 2003–2004 (2004 was a masting year) resulted of *rft* going to zero, or very close to zero, for about 6 weeks (Suppl. material 5, fig. 1[b]), while in 2004–2005 (2005 was a non-mast year) it was near zero for perhaps just 2 weeks, and shorter overall (Suppl. material 5, fig. 1[c]). In 2002–2003, for comparison, the also long dry season *rft* reached zero for a couple of days, and whilst many days had no rain the season was broken by three high rainfall events keeping *rft* just

820 below 100 mm (Suppl. material 5, fig. 1[a]). The relatively small decrease in mean daily
821 rainfall between 2005 and 2004 (Fig. 2) translated into a surprisingly large difference towards
822 the lowered SMC and suggested a non-linear effect, that is a little less rain led to
823 proportionally much more soil drying when rainfall was low-to-average.

824 **Caterpillar outbreaks**

825 In the latter half of December 2011, and again in the first half of March 2012, an
826 outbreak of a black caterpillar was observed that fed on young foliage of *M. bisulcata* trees
827 recorded for phenology in the P-plot. Although not quantitatively measured, the attacks were
828 extensive, as evidenced by the substantial amounts of falling frass, numerous caterpillars
829 hanging below the crowns on threads, and litterfall consisting of soft, green leaf tissues (G.
830 A. Neba and S. Njibili, pers. obs.). The same caterpillar was also recorded at another *M.*
831 *bisulcata* grove 4.2 km due south, in March 2012 (Norghauer et al. 2023). However, no visit
832 was made to that site in December 2011. Fallen caterpillars were also observed feeding on
833 young leaves of *Oubanguia alata*, a common understorey tree growing below *M. bisulcata*
834 crowns at Korup.

835 Also in the latter half of December, but in 2008, an outbreak of most likely the same
836 caterpillar species (an *Achaea* sp., probably *A. catocaloides*) had been recorded on *T.*
837 *korupensis* trees in the same P-plot (Norghauer et al. 2023). At that time, feeding upon *M.*
838 *bisulcata* foliage was limited to low levels on just those crowns closely adjacent to the more
839 heavily attacked ones of *T. korupensis*. Furthermore, and separately, at the end of January
840 2014 a morphologically different and larger species of caterpillar, yellow-green and behaving
841 very differently from the smaller black one, was seen on five of the 65 monitored *M.*
842 *bisulcata* trees (Suppl. material 6, text and fig. 1). Most probably it was another *Achaea*
843 species. Intriguingly, this caterpillar species was feeding on *M. bisulcata* flowers, not young

844 foliage. How influential the new insect herbivore was for *M. bisulcata* phenology that year is
845 uncertain because its distribution was localized to a 2–3-ha patch where the *M. bisulcata*
846 basal area was high.

847 **Tree phenology and masting intensity**

848 Tree phenology of *M. bisulcata* was compared between the heavy mast fruiting year
849 of 2010, and the year of 2012 in which fruiting was very low (Fig. 4; Suppl. material 2, table
850 1). Both time series covered the drought-defined dry season of that year and followed
851 changes in leaf-flush and leaf-fall (leaf exchange), and flowering, pod formation (green) and
852 pod maturity (brown). Attaining continuous fortnightly scoring was not always feasible and
853 each series has two gaps. Leaf flush likely began a little before the start of the time series
854 recorded for 2010, i.e. earlier than December 2009 (Fig. 4a), but was adequately captured for
855 2012 (Fig. 4b). The bulk of the leaf-flush happened within each year's dry season, flowering
856 well within it in 2010 but coming at the end in 2012. Even though the sum of the flowering
857 scores was similar in both years, pollination resulted in substantially more green and brown
858 pods in 2010 than 2012 (Fig. 4a, b). Caterpillars were not seen in the other years between
859 2009 and 2013, notably not in 2010. In 2010, green pods were apparent between 18 January
860 and 3 July, that is for 5.5 months, with a 1-month overlap as they turned brown between 5
861 June and 28 August, over 2.5 months (Fig. 4a). A similar time course was recorded in 2004,
862 and likewise (for green plus brown) in 1995 and 2000 (Fig. 4b of Newbery et al. 2006a).
863 Interestingly the overall period of pod formation was much shorter in the two back-back
864 years of masting 1997 and 1998.

865 Trees in 2012 suffered unusually in two definite caterpillar attacks by the same black
866 *Achaea* species, both coming just prior to peaks in leaf-flush (marked 'C' in Figs 1a and 4).
867 The earlier flush in early January 2012 was part of the annual leaf exchange process, but the

later one in early April 2012 not. The first was in part associated with the leaf fall around 15 Jan. 2012: 21 of the 61 trees lost new leaves then. The third leaf flush in late February 2012 (Fig. 4b) had no associated caterpillar attack. What happened in late March was unfortunately not recorded, but a building up of the re-flush starting then could be surmised if this event followed the same flushing patterns of the earlier and later ones. The sequence of events suggests that leaf flush in early January enabled the caterpillar population to initially increase, and that at the end of February there was a response by the trees to the first attack. The flush at the end of April is more difficult to explain. It could have been either a further delayed response to the first attack, or a direct response to the second attack, by a possibly now larger caterpillar population. The life-cycle dynamics of the herbivore would have allowed, however, only a second cohort of caterpillars to feed on that third and last flush for the year. The most flowering accompanied the middle leaf-flush peak in 2012, which speaks against caterpillars being around then because feeding on leaves might be expected to indirectly reduce flowering.

The presence of the black caterpillar in 2012 appears to have upset the smooth phenological stage-replacement of 2010, and led to a much-reduced reproductive output. The interval from the last year of full masting (1 year) was theoretically suboptimal, so likely the resource levels of P but not N were reduced and still below a threshold. A high N: P ratio may have helped the caterpillar outbreak. In addition, the masting pattern changed after 2011 (Fig. 1a), to the two moderate double-year form, possibly a carryover of the disruption of the feeding in 2012, and a destabilization of the proposed inherent 3-year cycle. In the dry season 2010, mean daily rainfall was 1.42 mm, yet the year prior it was 4.66 mm; correspondingly the rainfall for 2012 were 1.95 and 2.07 mm: prior-to-current ratios of 3.3 and 1.1 respectively. Interestingly, the lower caterpillar activity noted in the other grove to the south

892 was associated with average green-pod score of 1.7 in May 2013 (*n* = 33 trees; Suppl.
893 material 2, table 1), showing that masting was more intense there than in the P-plot that year.

894 The second herbivore attack in January 2014 of the other unknown caterpillar species
895 was before the second of the moderate 'm' mast fruiting of the double-years 2013–2014.
896 Much less is known about its effects particularly because detailed phenological recording did
897 not continue to end 2014. However, given that this species eats flowers, as well as young
898 leaves (Suppl. material 6) it most likely reduced the number of trees able to fruit that year,
899 even if the outbreak was contained to a far smaller known area than the successive outbreaks
900 of the black caterpillar in late December 2011 and early March 2012.

901 It is instructive, once again, to look at the course of rainfall events and *rft* during and
902 immediately after the dry seasons of 2009–2010 and 2011–2012 to find clues for the second,
903 early March, caterpillar attack. This last came during a second short dry period when there
904 was that unusual third leaf flush (cf. Fig. 4b with Suppl. material 5, fig. 2[c]). With an
905 interval of ca. 14 days between phenology census recordings, it is difficult to say which came
906 first; but the most likely explanation is the further dry period caused flushing and this
907 promoted renewed feeding, possibly from a next cohort of caterpillars that year. The dry
908 season 2009–2010 had also several dry days at a similar time but was broken by a large
909 wetting event (and there was no further flush after the dry season one). For comparison, the
910 pattern of 2010–2012 shows the shorter, later-starting and not so intense, dry season for a
911 typical non-masting year (Suppl. material 5, fig. 2[b]).

912

913 **Tree size-fruiting relationship**

914 Consistency in the intensity of masting over time at the individual tree level was
915 tested in the following way. Scores for brown pods in 2007 and 2010 were matched with

916 those for an equally strong masting in 1995 on a tree-by-tree basis. Score categories '0' and
917 '1' were combined. Fruiting was significantly positively associated in both cases ($\chi^2 = 10.61$,
918 df = 1, $P = 0.031$ and $\chi^2 = 10.28$, df = 1, $P = 0.036$, respectively). There is good evidence that
919 high- and low-scored trees tended to remain as such over a 12–15-year period, although
920 considerable between-trees variability existed.

921 Ordinal logistic regressions of brown pod scores per tree versus tree stem diameter (at
922 last census in 2005), in 2010, 2012 and 2013, or as fallen pods in 2014, were weakly and
923 insignificantly related though ($t = 1.40$, 0.45, –0.68 and 0.42, e.d.f. = 58 to 61, $P = 0.17$ to
924 0.60). As the phenology score was recording the *relative* proportion of a crown fruiting, this
925 meant that large trees did not have proportionally more pods than smaller ones.

926 **Oil palm yield comparison**

927 Access to fruit yield data for oil palm (*Elaeis guineensis*) growing in the estates of
928 PAMOL Plc on the eastern border of the KNP (Bulu-Mundemba, Ndian) allowed a
929 comparison with *M. bisulcata* mast fruiting under the same local climate conditions. An
930 analysis of the monthly yields, for 2003 to 2016, showed no year-to-year differences in
931 means attributable to changes in either rainfall or radiation, although there was a very clear
932 repeating pattern for each of the three variables within each year (Suppl. material 7, text and
933 fig. 1). Moreover, mast fruiting of *M. bisulcata* in this period (see Fig. 1a again) did not
934 correspond to peaks or lows in this proxy measure of productivity, for either the current or
935 prior year. This suggested that radiation and C fixation were not the primary drivers of mast
936 fruiting.

937 The poor relationship with radiation also means that yield cannot be used in an
938 inverse estimation to confirm the interpolated missing months of radiation at Bulu in 2009–
939 2011 (Suppl. material 1). The Ndian estates have the same substrate and soil type as southern

940 Korup. After initial trials in the 1960s through to the late 1970s, phosphate fertilization was
941 discontinued because little beneficial effect on palm fruit production was found (C. E. Etta,
942 unpubl. data). It is unlikely that much of the added P was still available in the soil by 2003.

943 **Stem increment growth and masting**

944 Annual radial increments (*incr*, mm) in stem growth of 20 cored *M. bisulcata* trees ≥
945 50 cm diameter in the P-plot from Newbery et al. (2013) were matched to occurrences of
946 masting over the 15 years of 1989–2003 (Suppl. material 8, fig. 1[a]). The end date was the
947 last year which had a reliably determined annual band for all trees. Standard deviation
948 increased linearly with the mean over years (slope [CV] = 1.14, adj. R^2 = 50%, P = 0.002),
949 indicating a considerable variability in increment between trees in any one year (Suppl.
950 material 8, fig. 1[b]). No masting was noted for 1988 (Newbery et al. 1997) but that is not
951 fully certain.

952 Linear mixed-effects models were run using ln(*incr*) as the response variable, trees as
953 subjects (or 'blocks') and ± 'M' as the factor. A binomial logistic regression fit of masting
954 versus increment was not feasible as the power, with only seven events in the period, was
955 low. There were no significant differences for increment in either the current year (F = 0.79,
956 df = 1, 279; P = 0.38), or in the year prior (F = 0.12, df = 1, 279, P = 0.72: increments
957 available for 1988), or in the year after (F = 1.90, df = 1, 259, P = 0.17). Thus, larger
958 respectively smaller increments were not associated with current mast fruiting, not (by
959 inference) caused by it beforehand, or conversely masting did not cause a change in
960 increment afterwards. Graphs of the increment series for each of 20 trees individually (not
961 shown) had no common correspondences with 'M' years, and the differences in mean
962 individual tree increment for fruiting type were highly inconsistent (+M: mean 2.49 ± SD

963 1.97, –M: 2.38 ± 1.98; differences 0.11 ± 0.77, range = –2.02 to 1.67). Mast fruiting appeared
964 little connected to stem growth in *M. bisulcata*.

965 Increment was positively correlated, however, with mean daily radiation in the
966 typically modal dry season period (using all records, i.e. 1984–2003), this 'quarter 1' being
967 defined by months DJF – (r = 0.507, df =18, P = 0.023), but not in the early and mid-wet
968 season quarters 2 and 3 (P = 0.32 and 0.41), although again in late wet season 'quarter 4' it
969 was (r = 0.479, P = 0.033). Fruiting would have been largely 50% over then, by mid-
970 September. For the year as a whole the correlation was also reasonably strong (r = 0.503, P =
971 0.024). Increment was not strongly correlated with rainfall in any quarter, nor overall (P =
972 0.12 to 0.70), and not with radiation in the year prior to masting (P = 0.10 to 0.73).

973 Binomial logistic regression fits of masting for 1989–2003 to mean annual core
974 increment with either *radi* or $radi_{sr}$ (current or prior year for both variables) were all
975 insignificant for the increment term (current: P = 0.49 to 0.63; prior: P = 0.46 to 0.95). The
976 same approach applied using increment of the year prior brought little improvement in fitting
977 (P = 0.18 to 0.33; P = 0.18 to 0.62, respectively). Thus, whilst increment and dry-season
978 radiation remained significantly positively correlated (r = 0.532, df = 13, P = 0.041),
979 partialling out a radiation effect was of little avail in unravelling a fruiting-stem growth
980 interaction. These new analyses on the stem increment data provided further important
981 opposing evidence for C not being the limiting factor for mast fruiting.

982 **Nutrients during the masting cycle**

983 The newly reported nutrient data, coming from the approaches described in the
984 'Methods' section above, are combined here with other nutrient data already published (see
985 citations within the footnotes to Tables 2 and 3). To begin with, for 1997 and 1998, and for
986 2011, the leaflet-to-rachis ratio of N was 1.568 and 1.524, and correspondingly for P it was

987 1.344 and 1.274 respectively, with means of 1.546 and 1.309. For 2011 only, the L/R ratios
988 for K and Mg were 0.540 and 1.686, respectively. It was striking how much higher the K
989 concentration was in the rachises compared to leaflets.

990 In the 1990–1992 litter sampling the bulked samples each represented 0.320 ha of
991 forest. In 2011 sampling the trap clusters represented on average 0.368 ha. This means that
992 each nutrient value is similarly based on ~ 1/3 of a hectare, and the respective samples sizes
993 of 5-and-5 versus 30 can be retained in statistical comparisons without needing to group the
994 2011 ones. Likewise, the 1997–1998 study used some of the same half-plots, and accordingly
995 had the same scale as in 1990–1992. Working with the typical masting cycle of 3 years
996 shown by *M. bisulcata* at Korup over the period 1989–2010 (Newbery et al. 1998; Newbery
997 et al. 2006a), the three sampling dates together allow a series of immediately-after (2010–
998 2011), and 1 (1990–1991) and 2 (1991–1992) years after (and thus also immediately before
999 the next), masting events to be constructed. The two consecutive years are likely temporally
1000 correlated, but the time difference between them and 2011 is large. The further data from
1001 1997–1998 present an interesting comparison in that masting in 1997 had evidently not
1002 prevented a repeat even the following year. Over the successive four fortnights,
1003 concentrations of N were 18.69, 17.20, 18.58 and 18.63 mg g^{-1}, and those of P were 0.802,
1004 0.799, 0.787, 0.956 mg g^{-1}.

1005 The concentrations across the three weekly litter samples in December 2002 (Schwan
1006 2003), were averaged per trap. To obtain whole-leaf concentrations, the averaged values per
1007 tree were first divided by the 1997–1998/2011 leaflet-to-rachis ratios to have indirect rachis
1008 estimates, and then the 4:1 leaflet-to-rachis mass ratio was applied. This assumed that the
1009 ratios from the 1997–1998 and 2011 studies could be used here for 2002 (which lay between
1010 them). For the complete five-element data sets and direct estimation of leaf concentrations in
1011 Table 2 (viz. 1991–1992 and 2011), years 1-3 after masting, N, P, K and Mg all differed

1012 strongly and significantly (F = 13.4, 12.2, 27.2 and 6.01, all $P < 0.01$) but not Ca (F = 1.0, P
1013 > 0.05).

1014 The results show that in the inter-mast period, N was low for the first two dry seasons and
1015 then rose the year before the next masting, P increased from low to high approximately
1016 linearly in the period, Ca barely changed, K and Mg were relatively high for the first two
1017 seasons but fell in the third before masting (Table 2). This suggested that N and especially P
1018 concentrations were depleted by the last mast fruiting and were re-instated before the next
1019 event. Both K and Mg increased earlier in the interval but were presumably deployed
1020 elsewhere before masting. Despite the different sampling approaches, standard errors of
1021 means, across years per element, were quite similar. The concentration within the double-
1022 masting period 1997–1998 intriguingly lay between the 1991 and 1992 ones for N, but were
1023 higher than both for P. That P was accumulating before masting is clearly demonstrated. The
1024 rise in P at the end of the litter fall series, but not of N, in 1998 is also remarkable (Table 2).
1025 The 1998 litter was collected immediately before a masting like the 1992 one, so they could
1026 be considered comparable in this respect even though the previous mast fruiting events were
1027 1 (unusually) and 3 years prior respectively. Averaging where possible values in Table 2 for
1028 2011 and 2002, and separately those for 1992 and 1998, gives composite estimates of leaf
1029 concentration respectively immediately post and prior to masting as: N: 16.73 and18.80
1030 (+12.4%); P: 0.615 and 0.825 (+33.9%); K, 5.00 and 2.44 (–51.1%); Mg: 3.42 and 2.53 (–
1031 26.0%). These inter-mast changes suggested that N and P were depleted by fruiting and
1032 restored for the next event – proportionally three-fold more for P than N, but the opposite
1033 occurred for K and Mg.

1034 Reproductive allocation of N, P, Mg and Ca was in the order of 8% to 16% (Table 3),
1035 but for K it was considerably higher at 37%. This last value can be traced back to the
1036 relatively high concentration of K in *M. bisulcata* pods, slightly higher than in leaves. The

fruit to leaf mass ratio reached almost 0.6 for K compared with < 0.2 for the other elements. These calculations do not include root allocation, however, because estimates for them are lacking, in terms of both root growth rate per year and root concentrations. Fruiting in *M. bisulcata* is much costlier in terms of K than of P. *Microberlinia bisulcata* leaf litterfall rates in the 12-month July-to-June periods of 1990–1991 (non-masting in 1991) and 1991–92 (masting in 1992) – found by integrating the areas under curves of litter fall versus time in Fig. 2d of Chuyong et al. (2000) – were practically the same (1710 and 1670 kg ha^{-1} yr^{-1}, respectively). Multiplying these values by their corresponding P concentrations (Table 2), led to a difference of 0.168 kg P ha^{-1} yr^{-1}, which is very close to 50% of the investment in masting in 1998 (Table 3), assuming that the mast fruiting that year was similar in intensity to the one in 1992.

DISCUSSION

Mast fruiting as a non-stationary process

If masting is driven by the 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,

1061 especially, given the late transient cycle stage of the stand (Newbery et al. 2013) and the
1062 varying climatic variables on all time scales ranging from years to decades and centuries
1063 (Nicholson et al. 2000; Nicholson et al. 2018). The inconstancy might be best understood in a
1064 novel way with a two- or three-factor threshold model, where C, P and K reach potentially
1065 different thresholds, simultaneously or sequentially. Thresholds themselves may not even be
1066 constant over time but relate to age, climate trends, and other tree-internal demands. When
1067 one of the resources reaches its threshold early, its effectiveness could be limited by the
1068 slower accumulation of another resource. The first resource will need to be stored or
1069 allocated elsewhere in the tree, even to then support the acquisition of the lagging resource.
1070 In time the second resource accumulates to a level that crosses a pre-set threshold, and this
1071 allows the first resource to come into operation.

1072 The allocations of C to mast fruiting in *M. bisulcata* are substantial. In the earlier mast
1073 fruiting event of 1995, 28 out of 30 trees recorded had fruits. The average number of seeds
1074 per tree was ~26K (maximum 92K). Using estimates of mean dry masses of seeds and pods,
1075 and mean numbers of seeds per pod, the total dry mass investment was 17 and 307 kg per tree
1076 respectively, summing to 324 kg per tree (Green and Newbery 2002). These per-tree masses
1077 translate to 53 plus 981 = 1034 kg/ha, ~55% the mass of average annual leaf-fall (Green and
1078 Newbery 2002). Applying the individual seed and pod masses to counts made for the 2007
1079 and 2010 events, for trees that had pods (Norghauer and Newbery 2015), gave 181 kg per tree
1080 in 2007 and 122 kg per tree in 2010. (Excluding the two zero-producers, output values for
1081 1995 were 346 kg/tree.) On this basis the investments per masting tree in 2007 and 2010 were
1082 52% and 35% respectively of that in 1995, illustrating an up to almost two-fold variation in
1083 masting intensity across these full fruiting events. Other more semi-quantitative scorings of
1084 masting across the rest of the time series suggest a similar range in reproductive output.

1085 Flowering is a precondition to fruiting, but the dependence is not exact. Heavy
1086 flowering was recorded in 1992, a mast year; but in 1991 there was also especially heavy
1087 flowering but no mast fruiting (Chuyong 1994; Newbery et al. 1998). In 1990 there was some
1088 low fruiting (flowering unmonitored), this coming though in the year after a main mast
1089 fruiting in 1989: further, 1993 had very little flowering and consequently almost no fruiting,
1090 and 1994 relatively high flowering but only scattered individuals fruiting (Green and
1091 Newbery 2001a, 2002). From the later, more detailed, phenology recordings, 1995, 1997,
1092 1998 and 2000 had strong flowering and were masting years, whilst 1996 and 1999 flowering
1093 was practically absent and had no masting (Newbery et al. 2006a). Whilst valvate bracteoles
1094 protect flower buds before anthesis, it is possible that the intense occasional shower could
1095 damage flowers enough to interfere with pollination. This is the surmise for 1991, two years
1096 after the 1989 masting: fruiting was probably checked and masting was delayed to 1992. In
1097 2004, the dry season started 43 days after 1 December 2003, on 12 January 2004 (Newbery et
1098 al. 2006a): recall that the dry season for a given year starts in December the year prior.
1099 Flowering peaked over the week before and after that date. But in 2012, the season started 21
1100 days in, on 22 December 2011, which was 1 month before flowering started in 2012, and
1101 ended another month later. (In both 2004 and 2012 there were no heavy showers that could
1102 have disturbed pollination in the first halves of those dry seasons.) These facets indicate that,
1103 firstly, occasional external and unpredictable influences can alter the processes behind a
1104 masting cycle; and secondly, the timing of flowering (also linked to the timing of leaf-
1105 exchange) can change by up to a month with respect to the start of the dry season. If internal
1106 tree nutrient levels do, via deterministic physiological mechanisms, trigger the flowering –
1107 which leads most often to fruiting at some level of strength (Newbery et al. 2006a), masting
1108 remains also subject to climatic stochasticity causing interference to pollination (may be once
1109 in 10–15 years) and variability in dry season timing and intensity (every year).

1110 Abortion of small immature green pods falling to the ground was not seen in the 29-
1111 year period. It remains possible that outside of the three more intensively recorded periods
1112 this phenomenon was missed. If in occasional years there was strong flowering, but no mast
1113 fruiting followed, then usually those trees that did develop any pods carried them through to
1114 maturity. The control of masting therefore most likely happens before flowering (see
1115 (Newbery et al. 2006a) for further discussion). After that seed failure is simply a chance
1116 unpredictable cost within the evolved life history schedule.

1117 **Nutrient resource interdependencies**

1118 Analysis of the seed and pod nutrient concentrations and amounts in relation to those
1119 in mature leaves indicated ratios of between ~ 0.1 and 0.2 for N, P, Mg and Ca, but
1120 substantially higher at 0.6 for K. This difference is very largely due to the low concentrations
1121 of the first four elements, and a much higher one for K in the pods. Pods collected were
1122 recently fallen. Caesalp pods are hard and rather water-repellent for several weeks, so it is
1123 very unlikely they adsorbed much K coming down in canopy throughfall (G. Neba, D. M.
1124 Newbery and G. B. Chuyong, in prep.), or were they leached to any extent. Had that been a
1125 cause of an increase, then Mg should have increased too, yet it did not. Presently it is difficult
1126 though to explain why so much K was being invested in pods. The comparative leaf K values,
1127 coming admittedly from a retranslocation study where replication of bulked samples per date
1128 was small, do closely match those of mature leaves of plantation-grown *M. bisulcata* trees
1129 (averaging ~ 5.8 mg $g^{-1;}$ at ages of 13 to 18 years; D. M. Newbery unpubl. data). Whilst
1130 ectomycorrhizas are strongly linked to P acquisition and uptake in the P-poor soils, K is also
1131 very low in availability at Korup (Gartlan et al. 1986), and the surface-soil root mat (with
1132 dense mycorrhizal networks) is an efficient collector of K (and Mg) coming down in
1133 throughfall (G. A. Neba, D. M. Newbery and G. B. Chuyong, unpubl. data). In plots at the
1134 same site, Chuyong (1994) found N, P, K, Mg and Ca concentrations of 13.8, 2.09, 6.41, 2.22

1135 and 3.50 mg g^{-1} respectively in *M. bisulcata* seeds that fell in 1992. Pods were not separated
1136 in the 1992 general collections but included within 'all reproductive parts' in the HEM plots,
1137 those with high abundance of *M. bisulcata* had a mean K concentration of 6.04 mg g^{-1}.
1138 Although other elements in fruits were albeit a little higher than for *M. bisulcata* alone in
1139 1998, the earlier data confirm the K values of interest well. Investing P in seeds would
1140 presumably be important to the survival of establishing seedlings up until the time they could
1141 become infected with ectomycorrhizas and link into the mycelial network. Could it be that
1142 also K, not P alone – as for some time thought (Newbery et al. 1988; Newbery et al. 2002), is
1143 a second key controlling element of masting in the Korup groves? Several indications suggest
1144 that P and K might act synergistically.

1145 The main pattern explaining the masting time series was the sequence of relatively
1146 wet dry season followed by relatively dry one. There was no evidence of water limitation to
1147 large trees in the dry seasons because of their ability to root deeply (Newbery et al. 1997;
1148 Newbery et al. 2009), so this points to a soil or nutrient factor governed by soil moisture
1149 content in the upper soil layer, where fine roots and ectomycorrhizas form a root-mat and are
1150 most abundant and active in nutrient cycling. What is it about relative dryness and wetness of
1151 the dry months that leads to these relationships? Possibly dryness affected the fine roots and
1152 ectomycorrhizas. The drier the dry season, then likely the more restricted the root activity
1153 under limiting surface soil water conditions; which would possibly signal stored P in the
1154 ectomycorrhizas to be moved to intermediate locations ready for fruiting, and less would be
1155 used in maintaining new root growth. In a relatively wetter dry season this root activity would
1156 continue longer and more effectively, so that any additional P stored in the roots would stay
1157 there and not be signaled away to fruiting. Nevertheless, the main mineralization and uptake
1158 occurs in early weeks of the wet season (Chuyong et al. 2002), and this would be similar each
1159 year once the soil water content was high enough. This dryness is thought to be a proxy for a

mechanism that triggers translocation, but it is one that cannot operate without the previous year acquiring more P and setting up a form of 'relay'. It is interesting that moderate 'm' events occur in double-years and twice later, mirroring the two strong 'M' years 1997–1998.

At Korup in the HEM plots, sand, silt and clay proportions were 77%, 9% and 14% respectively (Newbery et al. 1997). There exist very few published water content vs water potential curves for sandy loam tropical soils, but at a site in NE Brazil with a very similar physical composition to Korup, Fisher et al. (2008) found that a change in SMC (at 30 cm depth) from 20% to 12% (cf. the wet-to-dry-season change in Fig. 3) led to a decrease in soil water potential (SMP) from –10 to –100 kPa – which is very much higher than the generally accepted value of –1500 kPa where wilting starts. Such a translation across sites should however be treated cautiously because any SMC-SMP relationship is finely dependent on the exact physical composition of the soil (Or and Wraith 2002). Wilting of understorey treelets and shrubs, even in the strongest dry seasons, was very rarely observed at Korup. Nevertheless, the drying of the top surface soil with the root mat might still be expected to affect nutrient uptake capabilities in the dry season. In those dry months the surface leaf litter is definitely dried out, and in many places the sandy-loam soil just below the organic layer is visible, leaving the root mat exposed. The implied sensitivity of fine roots and ectomycorrhizas of *M. bisulcata* to surface soil water conditions might in part result from this species very pronounced buttressing and an extensive lateral root system lying just below the surface soil mat (Newbery et al. 2009).

A cycle of 3 years would most likely allow a restocking of P, not only enabling growth of other tree parts, but also storage of P in wood rays and roots ready for fruiting (as the model later explains). A 4-year cycle could arise but, *ex hypothesis*, that would need a sequence of two dry dry-seasons: none was recorded, however. The regression modelling gave an indication of year-to-year increases in radiation, and positive deviations from the

1185 smoothed trend of radiation with time. Changes were relatively small, radiation varied rather
1186 little from year to year, both for the dry seasons and the years as a whole. The additional
1187 radiation probably did not contribute to much increase in photosynthesis which would cater
1188 completely for the extra demand in years of masting, above the potential competition for C by
1189 leaves, stems and roots. Variation also in start and duration of the dry season, with the fairly
1190 steady daily radiation inputs, meant that there was probably sufficient radiation supplying C
1191 on top of tree storage, to meet the high dry mass investment in fruits. Carbon supply was
1192 therefore likely not the limiting factor to masting. One way to resolve this possible
1193 contradiction is to propose that, internal to the tree, there was strong temporal division in the
1194 allocation of C between rooting (one year, wetter) and fruiting (the next, drier). Further, the
1195 lack of a relationship between proportion of crown fruiting and tree size may be further
1196 evidence that C is not the predominant limiting factor for mast fruiting – contrary to what was
1197 originally suggested by Green and Newbery (2002), if it can be assumed that large trees store
1198 more NSCs than small ones. The lack of year-to-year differences in oil palm yield relating to
1199 radiation is also moderate evidence of C from photosynthesis not being so critical for their
1200 yielding either. Palms can store up to ~20% of their C in stems from year to year (Legros et
1201 al. 2009; Corley and Tinker 2016). The lack of correspondence between oil palm yield and
1202 *M. bisulcata* fruiting suggests no common climatic driver and points indirectly to nutrients as
1203 the key factor in the forest, though possibly not P alone since palms did not respond to P
1204 fertilizer.

1205 The very few studies on C and nutrients involved in mast fruiting of dipterocarps that
1206 have been made largely support the thesis of this paper. Defoliation and girdling experiments
1207 on branches of *Dryobalanops aromatica* trees by Ichie et al. (2005b) indicated that flowering
1208 drew on C stored in local branches and the filling of fruits came from nearby leaves. This
1209 confirms the many similar conclusions for temperate trees mentioned in the Introduction.

1210 Relative allocation of P to fruits was shown to be higher than of C and N for of another
1211 masting dipterocarp, *Dipterocarpus tempehes* (Ichie et al. 2005a), again emphasizing the
1212 importance of P in reproduction, especially on P-poor tropical sites. During a different
1213 masting event for *D. aromatica*, Ichie and Nakagawa (2013) found that P concentrations in
1214 branch, stem and roots steadily decreased during flowering and fruiting (but not in twigs and
1215 leaves), N fluctuated slightly (in all parts) and, whilst K decreased during flowering, it
1216 increased during fruiting (in all parts). Of the P needed for fruiting, 68% was estimated to
1217 come from branch storage, compared with only 20% for N and very little for K. This was the
1218 first time root-stem-branch stored P was shown to be important for masting, and the result
1219 corroborated the hypotheses of Henkel et al. (2005) and Newbery et al. (2006a). A further
1220 study at the forest stand level provided more support for P and K both being key nutrients in
1221 mast fruiting. Aoyagi et al. (2018) followed nutrient fluxes in soil, stems and fine litter in a
1222 lowland dipterocarp forest during one such event and for 4 years afterwards. Fluxes of P and
1223 K were much higher in total fine litter in the mast year than later years, whilst those of N, Ca
1224 and Mg altered little; the higher P and K was coming from the high allocations to fruits.
1225 Interestingly, P and K concentrations in coarse roots – but not stems – of the most abundant
1226 dipterocarp, *Shorea multiflora*, decreased more in flowering than non-flowering trees. This
1227 might indicate root storage of P and K ahead of stem and branch storage, in preparation for
1228 fruiting. Kitayama et al. (2015) have more generally demonstrated in NE Borneo that across a
1229 P-use efficiency gradient, forest trees allocate proportionally much more P than C or N to
1230 reproduction (in relation to total allocation), even at P-poor sites.

1231 **Masting and carbon supply**

1232 The internal distribution of C between potentially competing sinks within each tree
1233 has a further interesting aspect. A majority of the *M. bisulcata* trees in the grove are presently
1234 of large to very large (≥ 50 cm stem diameter) sizes which means they likely have

1235 considerable respiration and maintenance costs. Carbon at least would not be so readily
1236 available in an average year to sustain such a heavy fruiting without causing deficits in
1237 growth elsewhere in the tree, perhaps in fine root and ectomycorrhizal production. This
1238 would lead, hypothetically, to an even stronger competition between rooting and fruiting,
1239 once stem growth is partitioned aside. That seedlings and saplings survive very poorly close
1240 to adults, led to the proposal of a reverse drain operating towards the old adults especially in
1241 mast fruiting years, for P as well as for C (Newbery et al. 1998; Newbery et al. 2006b;
1242 Newbery et al. 2010; Norghauer and Newbery 2016).

1243 Previous estimates of leaf litterfall were 1880 and 1380 kg ha^{-1} yr^{-1} in non-masting
1244 1990 and masting 1989 respectively (the first estimate is used in Table 3), and came from
1245 Green and Newbery (Green and Newbery 2002), who in turn based their calculations on
1246 January-to-December, plot-level, leaf litterfall estimates given in Newbery et al. (1997). The
1247 1990–1992 data later indicated 39% of that litter was from *M. bisulcata* trees. This 0.74:1
1248 ratio may have been an overestimate, because it used calendar year estimates which would
1249 have missed linking November-December litterfall with that in January to April prior to
1250 masting, and the newer 1990–1991 species-specific data were more precise. Or it simply
1251 reflects variation in litterfall, viz. 1380, 1880, 1710 and 1670 kg/ha over the four years 1989
1252 through 1992, which suggests that C supply was likely again not to have played an important
1253 role in determining mast fruiting since in around one masting event there was an implied cost
1254 to leafing and around the other none. The fruit-to-leaf amount ratios and reproductive
1255 allocations percentages in Table 3 may well be ~10% lower than the true values, if the 1990–
1256 1992 litterfall estimates did apply. The 1990–1992 data also display a small shoulder in May
1257 1992, possibly the result of the last older leaves being exchanged for the new green pods.

1258 Green pods stay on the trees for more than 5 months and therefore will contribute C to
1259 their structures and to developing seeds. This is likely an important source, and pods and

1260 seeds may indeed be almost autonomous in this respect. Pods are also held up high on the
1261 outer canopy edges where their photosynthesis is maximized (Norghauer and Newbery 2015).
1262 Bennett et al. (2011) reviewed the role of pods in their photosynthetic capacity, and Zhang et
1263 al. (2017) provide a detail analysis of C balance in the pods of *Medicago sativa* to show the
1264 considerable C inputs that are possible. This source of C would make the *M. bisulcata* trees at
1265 masting even more independent of C stores within the rest of the tree. It could explain the
1266 effect of raised radiation in the current fruiting year when compared with the one prior.

1267 That stem increment growth was positively related to current year radiation, but mast
1268 fruiting was not always, or at least not so strongly, suggests that C from photosynthesis was
1269 being used for stem growth and in mast years it was additionally contributing to mast fruiting.
1270 An internal trade-off between root growth plus ectomycorrhizal activity to enable the uptake
1271 of nutrients allowing nutrient uptake, and an allocation to fruits and seeds when cued, may
1272 probably well be the basis to the masting cycle. In the year following a masting, relatively
1273 more C would be allocated to roots because, if fruiting is 'switched off', roots become the
1274 main alternative sink; and then if in the second year there is sufficient P to cross the
1275 threshold, with some increase in radiation and extra C input, a next masting would occur after
1276 2 years. If P accumulation was limited the tree would wait until the next year, forming a 3-
1277 year cycle. Extra C available in that second interval year might then determine the intensity
1278 of the masting ('M' or 'm'). A notable difference between P and K, is the rate of change in
1279 concentration in the leaf litter as the interval between mast fruiting progresses: P increased
1280 slowly over 3 years, but K rose rapidly then fell lower than at the start. This hints at faster
1281 recycling of K than P, with a stronger withdrawal of K than P at senescence later as storage
1282 cells were being refilled prior to masting.

1283 **Rainfall and nutrient uptake**

The 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, which is up until the 100 mm threshold defining the season is exceeded. The first week's rainfall governs root growth and ectomycorrhizal physiology, and the later ones connect to the early wet season and the throughfall which primes the start period of optimal leaf litter decomposition (Chuyong et al. 2002, 2004). A dry season may well limit root activity, and it also would delay decomposition: one which was short would only affect the former. On the other hand, a relative wet dry season will be expected to restrict rooting and ectomycorrhizal activity much less and encourage the earlier start of decomposition, both processes leading to better nutrient uptake into the trees. Ectomycorrhizal activity doubtless plays a role in P uptake, and the regrowth and maintenance of the root mat itself determines the level of retention of K leached from the canopy and its uptake.

An intriguing aspect in connection with the P-supply for fruiting is how P gets taken up and stored in inter-mast years. In the dry season of 1988–1989 and 1990–1991 there were pronounced peaks of P in fallen leaf litter in the HEM but not LEM plots (Newbery et al. 1997). This peak was absent in 1989–1990, directly after the heavy mast fruiting. The HEM litter would have been composed of ~80% *M. bisulcata* leaves (Chuyong et al. 2000). In a relatively dry dry-season with likely more die back of fine roots and ectomycorrhizas than in a wetter one, P might be translocated out of these fine roots and ectomycorrhizas, going into storage for fruiting. Altogether, the integrated aspects of this P nutrient cycle do provide reasonably strong support for P storage and use leading up to, and during, the masting events as proposed by the original PACER hypothesis.

Another result providing important evidence for P-storage is from the comparison between concentrations and amounts in the years across masting intervals which suggests further that the 50% of P used in masting was coming from retranslocation of P out of

1309 senescing leaves a few months before. This P was probably being stored in branches. By
1310 difference it might be deduced that the other 50% was older and coming from local
1311 branch/wood storage built up in the prior 1 or 2 years, still within the interval. That result
1312 would fit with the notion of a temporary store for P and not all of the P needed for masting
1313 could be supplied in the current year alone. Rosell et al. (2021) in a study of a range of
1314 tropical tree species found the inner bark of branches was especially important for NSC
1315 storage and, although not yet tested, this may be where P is also held, ready for fruiting.
1316 Jones et al. (2019) indicate this as a possibility for premontane tropical forests.

1317 If P in leaf litter is relatively low in concentration after allocation to fruiting (Newbery
1318 et al. 1997; and new evidence in this paper), then the fast-forward cycling proposed by
1319 Chuyong et al. (2000) could be temporarily slowed because mineralization by saprophytic
1320 fungi would have a low-litter resource to decompose. Root activity would either need to
1321 become more intense and efficient to take up the now lower soil levels, or at this time the
1322 ectomycorrhizal activity would come more to the fore by not only accessing low molecular-
1323 weight organic P molecules efficiently but also by effectively reaching low-concentration
1324 inorganic P sources further way from roots. This impasse would strongly select for the
1325 several co-adapted root mat and ectomycorrhizal traits seen in the field in order to achieve
1326 restocking of P. The rise in P accumulated just before masting could lead to higher P in litter
1327 falling that year which on one hand would mean fast re-uptake but on the other appears to be
1328 a dissipative risk when the perceived strategy is to save P (in the tree) for immediate use in
1329 fruiting. However, the ectomycorrhizas being part of the whole tree system, and cycling
1330 highly efficient, P is being 'saved dynamically' within the nutrient cycle. Also, N and K
1331 would in parallel complement C in stores – the latter benefitting from the small increase due
1332 to radiation enhanced photosynthesis, all three also needed for seeds and pods. That P was
1333 high in falling litter just prior to masting might furthermore indicate that P stores were quite

full after a 2-year interval, and some of that 'extra' P was also coming from root retranslocation.

The analysis of mast fruiting in 1989–2004 (Newbery et al. 2006a) used 150 trees across the whole P-plot, but the later recording 2009–2014 used a subset of 61 trees in the eastern half, an area 100–500 N by 1000–1200 E, on the higher ground with denser stands and larger trees. The masting time series could potentially have been confounded by sampling extent changing over time, because for the earlier half (1989–2004) it was found that masting was significantly stronger on the relatively higher and drier sites of this eastern part of the P-plot compared with the rest of the plot (Newbery et al. 2006a). Allaying these doubts, the full and strong masting in the second half (2007 and 2010) were confirmed by seed trapping across the eastern 25 ha of the plot (Norghauer and Newbery 2015). The two double years, in the second half of the time series, were only moderate masting despite being at the more favorable topographic location.

The very strong masting achieved by *Dicymbe corymbosa* in Guyana, with 3–4 t dry pod and seed mass per ha, were associated with pronounced El Nino Southern Oscillation (ENSO) peaks in radiation (Henkel et al. 2005; Henkel and Mayor 2019). However, this ectomycorrhizal detarioid, although phylogenetically very close to *M. bisulcata*, is unusual in that it reproduces annually also by sprouting, which must impose a considerable demand on C and nutrients for growth. For this reason, it might be conjectured that C stores are probably being continually used up and hence, to achieve a mast fruiting, a dependence on an additional boost of incoming radiation in those ENSO years would be necessary. Again, in contrast to most African detarioids (including *M. bisulcata*), *Gilbertiodendron dewevrei* – which forms monodominant stands in Central Africa – exhibits mast fruiting which is spatially unsynchronized and at irregular intervals (Hart 1995). Its individual seeds are very heavy (~30 g), so the mass allocated to reproduction per tree is probably far greater than for

1359 *M. bisulcata*. Compared with SE Asia and C. and northern S. America, the lack of a strong
1360 ENSO signal in C. Africa is pertinent (Poccard et al. 2000; Camberlin et al. 2001). Masting in
1361 dipterocarps may well be for different suite of factors from those controlling the detarioids,
1362 achieving an evolutionary stable strategy along an alternative channel.

1363 **Interference effect of herbivores**

1364 The loss of a 2- or 3-year cycle in masting after 2011 suggests that the rhythm of
1365 wet/dry dry-season release of nutrients needed for full masting was disrupted by a
1366 combination of lack of an alternating pattern in rainfall plus heavy caterpillar attacks. This
1367 latter unforeseen intervention, combined with an unusual climate regularity over 3 years,
1368 acted as a 'quasi-treatment' in that C gain and storage were likely temporarily reduced. From
1369 the above argumentation it was not so much the decrease in C to supporting fruiting that was
1370 alone important but also the loss of C input for roots to allow P to be taken up and
1371 accumulated even in the relatively wet dry seasons. With some commitment to flowering
1372 already, leaf grazing would have nullified any C input from the local branches attacked to
1373 fruiting, requiring the tree to draw on stores in the branches. Nevertheless, some fruits
1374 resulted, indicating a means by which tolerance to herbivory could have occurred (Norghauer
1375 et al. 2023). The caterpillar attacks may have interfered with the accumulation of P and
1376 thereby interrupted masting in full, leading to the unusual double 'm' years. The evidence of
1377 an herbivore effect is strongest for fruiting in 2013–2014 because of the detailed phenology
1378 data in 2011–2012. It is tempting to suggest that something similar might have been
1379 happening in 2015 before the very similar masting pattern of 2016–2017: alas, herbivore and
1380 tree phenology records were not possible during those later 3 years. A further unknown
1381 aspect is how herbivory may have induced stress hormones in the trees which, interacting
1382 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 densities at ~ 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 over recent decades (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 and 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 same reason for the yellow-caterpillar given the extensive multi-decadal phenological monitoring of *M. bisulcata* (Newbery et al. 1998; Newbery et al. 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 on the dry months and early wet season when caterpillars would occur, did not record them. Whether these outbreaks are triggered by favourable climate factors, or palatable leaf chemistry or less parasitoid pressure, either perhaps induced by drier conditions (Van Bael et al. 2004) or simply mounting abundance over years (Wong et al. 1990), is unknown. Herbivore attacks to flowers, occurring stochastically, might be viewed as being similar in end effect to intense rainfall events disrupting pollination: both limit reproduction.

Refined updated hypothesis for mast fruiting in caesalps

1407 The mast fruiting cycle in *M. bisulcata* could thus be explained in terms of the
1408 availability of three principal resources which govern the timing of reproductive output: the
1409 limiting resource P, water as a controlling resource, and C as a qualifying resource. If
1410 sufficient P accumulates within 2 years to trigger flowering and there is sufficient C coming
1411 from storage laid down over the last year or supplemented due to a positive radiation
1412 difference between prior to current year, then fruiting is to be expected. But when P is slower
1413 at accumulating, the interval is extended by one year and fruiting happens within 3 years. It is
1414 highly likely that in the latter case C would still be sufficient either from reserves laid down
1415 in the tree in the previous year and/or a small surplus the current year of fruiting. When there
1416 is sufficient P accumulated after one year but not quite enough C for a full masting, fruiting
1417 may follow anyway at a moderate level; and in doing so it is likely that not all of the
1418 accumulated P would have been allocated 'as planned', and the part remaining, plus last
1419 year's continuing uptake, will sustain a second moderate fruiting. According to these resource
1420 requirements, it is difficult to see how the pattern could be 'm-M' or 'M-m', and neither of
1421 these were observed: in the first, there would be insufficient time after a 'm' fruiting to build
1422 up P so rapidly to have an 'M' one, and in the second, the 'M' first would exhaust P levels
1423 down below a threshold and no 'm' would likely be possible either. The pattern M-M did
1424 occur once, however, at the time of an exceptional rise in radiation levels over a 3–4-year
1425 period: it can only be hypothesized that there was unusually even more surplus C for extra
1426 root growth and P uptake in both the year preceding the first 'M' year and during the second
1427 one. The main processes leading to mast fruiting in *M. bisulcata* are schematically shown in
1428 Fig. 5.

1429 An interesting aspect is the feedback control that might operate by way of C going
1430 either into fine roots and ectomycorrhizas, which would enhance nutrient uptake, or into
1431 wood storage (stem, branch and large root), which could sustain a next fruiting. The 2- or 3-

year cycle is simply a consequence of the contingent conditions of these trees growing in low-P soils aided by ectomycorrhizas. Rainfall and radiation are stochastic processes, to some extent inversely related, which overlies the intrinsic deterministic cycle: the important difference between them is that rain, acting primarily on the soil, facilitates P release, acquisition and uptake (needed to accumulate P), and whilst C is needed also for fruiting, it is essential for root production and maintenance of ectomycorrhizas that makes this P uptake possible. That root growth should always precedes fruiting in a masting year, the first in late-dry into early wet season (March–April), the latter in late wet season (September–October) decides the sequence unambiguously: C in the dry season will go to the root sink first and what remains stored, used for stem growth or reserved for fruiting when it happens. The low P supply is therefore the main determinant: C must be sufficient but does not appear to be decisive for the interval length. Although N and K will also be involved 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, simplified reductionist approaches do not recognize the integrated nature of growth and reproduction. Carbon (sugars) and K are required for transport and storage, while P is 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

1457 physiology requires an integrated and dynamic approach, one of shifting sink strengths over
1458 time. After a last masting, roots would likely act as the strongest sink, then the stems (and
1459 rays and bark) and branches – part growth, part storage – and finally reproductive parts. No
1460 abrupt switches in C, in contrast to a threshold switch for P, but a gradual altering of the
1461 components over a 2–3-year cycle occurs. For this to operate it is necessary to hypothesize
1462 feedback from the C-depleted branches to the more C-depleted roots. With the fruiting sink
1463 removed, C should move from stems to roots. Whether this needs additional hormonal
1464 control is an interesting question. It remains a conundrum as to why 'in the background' to
1465 the rooting-fruiting axis, stem wood growth is positively correlated in a quasi-independent
1466 way with radiation. Stems may be working perhaps as the storage stabilizers, being placed
1467 centrally between shoots and roots. As they grow, they store and balance the terminal
1468 demands. The levelling adjustment of C between the first and second interval years could
1469 perhaps explain the lack of clear correlation between fruiting (and inversely rooting) with
1470 stem growth increment. The time sequence within the year is also important here. In the
1471 second (drier) year of fruiting, C is not, *ex hypothesis* predominantly going to roots in the
1472 early wet season but more to stems for storage, and en route there for filling fruits later in the
1473 wet season (Fig. 5).

1474 If radiation were to increase during an increasing part of a cycle or as a longer-term
1475 trend, and C were alone the limiting resource for masting, then fruiting would come closer
1476 together and this would defeat the putative economy-of-scale selection. In this respect a non-
1477 stationary time series offer advantages when matched to an also non-constant climate
1478 environment. On this basis it would seem also unlikely that C could be the key resource for
1479 *M. bisulcata*. Further, C available per tree will decrease with tree age after the point of
1480 maximum crown extension because of the higher respiratory loads incurred in maintenance of
1481 the whole tree. This may be connected with the observed crown thinning of the largest trees

1482 (J. M. Norghauer, unpubl. data). When seed production was substantial, in proportion to the
1483 high flowering per crown then there would be a deficit of C to fill pods, or pod production
1484 would decrease, or another cost incurred (e.g. at the roots or wood production). But the
1485 evidence was that in *M. bisulcata* the relative crown-cover with pods remained constant with
1486 size and, by broad inference, age. As a tree grew to have a larger root system with
1487 ectomycorrhizas to maintain, to acquire P and retain K, when absolute pod and seed output
1488 rose then the demand for P and K would have also. As with C and N, we can expect that P
1489 and K is stored in 'quick-release' forms in wood rays and bark of the stem and the main
1490 branches. A phenomenon often remarked is of one part of a large crown flowering and
1491 fruiting much more than the others, which could be explained by a correspondingly more
1492 active root system of the tree, and a matching storage of nutrients in the wood and branches,
1493 on that side: see Newbery et al. (2009) for the strong crown asymmetry in *M. bisulcata*.

1494 The arguments going from nutrient concentrations in fallen litter through to the
1495 possibly the trees building up and storing P and K before masting are tenuous because of the
1496 many uncertainties about the processes involved. If some translocation occurs out of leaves
1497 before they are shed, then why are the P levels so high just before masting? If P was being
1498 actively stored for fruiting, it might be expected that it would be lower in concentration in the
1499 fallen leaves. However, the high concentration reflects that all the trees were well stocked
1500 with P by that time, the stores were full, or even over-full, and there was still plenty of P to
1501 fall. From earlier work, it was established that ectomycorrhizal species, especially *M.*
1502 *bisulcata*, drop P-richer leaf litter than non-ectomycorrhizal ones (Newbery et al. 1997) partly
1503 because the retranslocation was less (Chuyong et al. 2000), and it was argued then that this
1504 allows the decomposition process to operate without P limitation, the 'fast forward' strategy.
1505 However, the concentration of K (to a lesser extent that of Mg also) reached a peak mid-
1506 interval and then fell just before masting. This could mean that K was being translocated into

storage before fruiting. In general, the export of K and Mg from leaves of trees is usually low compared with that of N and P. Understanding the differences in dynamics of P and K in this context is highly challenging, and also explains why N showed no clear mast-interval trends. Whilst K was likely building up on soil colloids in wetter dry seasons, mineralized from fallen leaves, dead roots and old pods during decomposition, and that this process was more limited in the drier dry seasons, suggests that K must also have been transported and actively stored in the tree between the prior and mast years. To recycle more K via litterfall would involve a potentially high loss due to leaching when the cation exchange capacity of the soil has already been reached, compared with the seemingly tighter and 'safer' direct access by ectomycorrhizas to organic P. This reliability aspect therefore favours P over K as the better controlling factor in masting (Fig. 5).

Phosphorus storage and control

What could the likely form of storage of P in trees be? Since Bieleski (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. Yet 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

1532 conceivable that the same mechanism could operate in seasonal tropical trees and even be a
1533 basis to P storage for mast fruiting species. How inositol hexa*kis* phosphate is linked to
1534 polyphosphate formation in roots and mycorrhizas and comes under hormonal control
1535 remains unclear.

1536 In an experiment with *Eucalyptus grandis* seedlings, comparing low and high P
1537 media, Mulligan (1988) detected stored P in the form of esters and residual P (mostly
1538 phosphorus proteins), especially in roots, and more so the low P medium. The idea is that
1539 these stores buffer the plant (maybe actively stored), from there P can be mobilized and sent
1540 to other stores in the shoots. In a similar vein, Netzer et al. (2017), comparing mature *Fagus*
1541 *sylvatica* stands – one on high and one on very-low P available soils – found that in the latter
1542 P built up in roots in late summer, and from there was moved on to stem and branches,
1543 suggestive of at least two storage sites in a series enabling adaptation to the poor site.
1544 However, hardly anything is known about how P stores are internally controlled, or how
1545 hormones signal transfers of P (Rennenberg and Herschbach 2013), which could give even a
1546 lead as to how P might be built up in stores in masting intervals, and once a threshold level is
1547 met how the switch to flowering is signaled.

1548 Much evidence suggests that senescence in leaves, and possibly pod formation, may
1549 also involve cytokinins (Marschner 2012). Chiou and Lin (2011) have proposed different
1550 hypothetical models for inorganic P being regulated by cytokinins and sugar levels. How
1551 these promising models can be extended to storage and release of P has yet to be worked out.
1552 The strongest candidate for the elusive 'florigen' is now widely held to be a flowering locus
1553 T [FT-] protein, which again appears to be controlled by a cytokinin (Turnbull 2011).
1554 Cytokinins act at long distances throughout the plant and are bidirectional in their effects,
1555 both of which might hypothetically implicate them in inositol hexa*kis* phosphate metabolism
1556 and P storage. It remains likely that floral initiation in *M. bisulcata* takes place at the end of

1557 the wet season, before leaf exchange occurs in the dry season (see discussion in Newbery et
1558 al. 2006a). Earlier results on cultivated apple (*Malus*) trees suggested already that a two-way
1559 process of hormonal control could be operating (Davis 1957), and the idea that sugars and
1560 other NSCs destined for the usually stronger root sink (Goldschmidt and Golomb 1982, for
1561 mandarin (*Citrus*)), (Hansen et al. 1982; for prune (*Prunus*) on K-deficient soils) might be
1562 diverted to the flowering meristem sinks under the control of gibberellins (Sachs 1977). How
1563 exactly the 'switch' occurs remains elusive (Monselise and Goldschmidt 1982), and still to
1564 this day. The precise consistency of alternate bearing in pistachio (*Pistacea vera*) orchards
1565 has been questioned though, on statistical grounds (Rosenstock et al. 2010).

1566 **Active storage hypothesis**

1567 Storage of C as reserves in trees (stem rays, bark and branch wood) was widely seen
1568 in the past as being passive. The C was being made available for regular annual growth
1569 processes in ways that optimized the economy of the tree (Zimmerman and Brown 1971).
1570 Extending this idea to nutrients, Chapin et al. (1990) produced a systematic table for N and P,
1571 reserves of the latter mainly featuring as inorganic phosphate, polyphosphates, or
1572 phospholipids, leading them to conclude that dependence on mineral nutrients is likely much
1573 more pronounced than it is on C for reproduction. Sala et al. (2012a) argued that the build-up
1574 of NSCs in stores in trees might be acting as a buffer against stochastic variation in C inputs
1575 due to environmental stresses (e.g. drought, herbivore attacks), which as a bet-hedging
1576 strategy would insure against temporary collapses in maintenance and growth. The storage
1577 would need to be active, rather than passive, otherwise in the latter case it would be used up
1578 immediately in extra current growth. Extending this idea to mineral nutrients, Dietze et al.
1579 (2014) hypothesized that N, P and K might also be accumulated and stored to guard against
1580 periods of reduced nutrient uptake, stabilizing the internal nutrient cycles. Hormones might
1581 therefore control source-sink processes actively. The empirical evidence for active vs. passive

control of C storage in trees still remains weak and unresolved though (Hartmann and Trumbore 2016). But where P and K especially are limiting growth, evolution of such an active mechanism could be of considerable evolutionary advantage. Mast fruiting imposes a quasi-unpredictable (partially stochastic) demand on mineral nutrients supplies, and therefore for P and K active storage would serve it well, particularly in sites where uptake patterns themselves are subject to environmental stochasticity (the intensity of the dry season at Korup, for example).

Nutrients in alternate bearing of tree crops

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

1607 masting years (G. A. Neba, D. M. Newbery and G. B. Chuyong, unpubl. data). How far K
1608 might be transported laterally in the mat by mass flow is unknown.

1609 Picchioni et al. (1997) further showed, for pistachio again, that N and P were
1610 translocated out of the mature pericarp into the seeds of the same fruits, although K was not,
1611 which left the pericarp relative rich in K on fruit fall (harvesting). This could have been
1612 happening in *M. bisulcata*, and in this way explains the K-rich pods. Possibly as pods
1613 browned they too moved N and P to the seeds. With K having achieved its role in aiding
1614 sugar transport (under the hypothetical hormonal control suggested), it would then be
1615 redundant as regards reproductive investment *per se*: the fallen pods would be leached much
1616 later by the end wet season rains, even some remaining until next year, and in this way
1617 returning the extra K to the forest floor and soil colloid sites. Returning to the question of
1618 possible CHO storage in 'off' years, direct estimates showed that very little of the stores laid
1619 down in those 'off' years (8%) contributed to the 'on'-year yield (Stevenson and Shackel
1620 1998) – confirming again the general finding mentioned above in the *Introduction*. Overall,
1621 the main evidence is in favour of nutrients plus hormones being the controllers of alternate
1622 bearing and, in extension, masting in forest tree species where nutrients are limiting.

1623 **Soil nutrient status**

1624 Nitrogen supply has been shown to be important for fruiting in *Nothofagus* (Smaill et
1625 al. 2011). In either N-fertilized stands, or unfertilized ones when rainfall was high (allowing
1626 higher N mineralization), masting was enhanced, subject to a temperature cue also operating.
1627 Likewise, Leeper et al. (2020) showed in N-poor sites, that masting of spruce was less
1628 frequent and less intense than at N-rich sites. Cone production was positively correlated with
1629 soil N in the year prior, not the current one. Both studies found lagged N-effects, implying
1630 that N was being stored. Nevertheless, unravelling the causes is difficult because the better,

wetter, conditions one year for N supply are not conducive to floral initiation, which depends more on warm drier ones affording higher sugar transport to apices. An inherent inverse correlation often exists which leads to an unstable alternation: a similar pattern is proposed for *M. bisulcata* at Korup with the relatively wetter and drier dry seasons.

Evidence for depletion of nutrients during masting, needing then a restocking for the next event, is unfortunately limited. For white-bark pines, Sala et al. (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 the PACER hypothesis and the main thesis of the current paper on *M. bisulcata*.

Climate factors which affect nutrient resource availability driving masting was a central argument of the review by 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. (2006a). 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. 2017). 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 might, in part, be achieved via a shared mycorrhizal network. It is a

working hypothesis that requires testing in the field at Korup. Given the lack of support for C storage being important for mast fruiting, clearly the C budget model of Isagi et al. (1997) needs to be rethought in terms P uptake, storage and usage.

Fernandez-Martinez et al. (2019) recognized that many mast fruiting species grow in N- or P-poor soils, or at least on sites where the demand for these elements is high. The authors relied on foliar N and P concentration data. There are two problems with this approach: firstly, from among the masting species some samples may be from mast years, others from inter-mast ones pulling the differences between masting and non-masting species apart; and secondly, many species well adapted physiologically to nutrient poor soils do have nutrient levels similar to those on richer soils but display different nutrient dynamics. Again, the obvious association with, and role of, ectomycorrhizas was overlooked. Contrary to the claim of Kelly (2020), nutrients can be hypothesized to determine masting when both their availability fluctuates, and their tree nutrient concentrations are synchronized via the mycorrhizal network. Stronger competition between masting and non-masting neighbours need not be invoked, as was proposed by Fernandez-Martinez et al. (2020). It follows from ecophysiological adaption of the masting species to their nutrient-poor conditions. From the nutrient-supply model the other economy of scale factors can operate; in the case of *M. bisulcata* this would probably be mainly to satiate seed predators (Norghauer and Newbery 2011).

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

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

Tree-tree root connections

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

1706 buttressing – and temporarily supporting suppressed, damaged or dying neighbours, other
1707 advantages of root grafts have not been so obvious (Loehle and Jones 1990). However,
1708 synchronizing nutrient supplies between, and storage within, trees across whole clusters
1709 would clearly be beneficial and strengthen masting. Root grafts would moreover provide a
1710 strong 'platform' for the ectomycorrhizal network and faster local transfers. A role for root
1711 grafts enabling masting has recently been suggested by Noble et al. (2018) to partly explain
1712 alternate bearing in pistachio in a year when pollination synchrony (the Moran effect) was
1713 relatively weak. The focus in that plantation study was on C as the putative resource being
1714 transferred.

1715 More directly relevant to *M. bisulcata* was the 1953 work of Yli-Vakkuri, cited by
1716 Bormann (1966), showing that P was moving across root grafts of *Pinus sylvestris*: the author
1717 made no connection to ectomycorrhizal status of pines or association of ectomycorrhizas with
1718 mast fruiting (see Newbery 2005). Conceivably, ectomycorrhizal and grafted root-networks
1719 might operate together within *M. bisulcata* tree clusters, either contemporaneously or in
1720 successive phases around the end of the dry into the early wet season. If hormones are also
1721 transportable across grafts, an added level of synchronizing control is afforded. The role of
1722 tree root interconnections (ectomycorrhizas and grafts) becomes an essential auxiliary to the
1723 main masting hypothesis. Bormann (1966) advanced the thesis that root grafts were
1724 established first by alignment of xylem tissues which rerouted water flow, and connecting
1725 phloem tissues permitted organic and nutrient transfer later. Between the mid- and late-
1726 ontogeny stages, *M. bisulcata* trees growing in dense patches become large adults, as
1727 described by the transient dominance model (Newbery et al. 2013), and root grafting may
1728 have started when water was at a premium in the dry season. It then changed to having a
1729 more organic-flux transfer role once deep roots had secured all-year-round water supplies, the
1730 root mat had fully formed, the litter nutrient cycle was stable, and P (and possibly K) were by

then in greater demand for growth and reproduction. To know whether or not codominants *Tetraberlinia bifoliolata* and *T. korupensis* graft below ground onto *M. bisulcata* would be interesting. That the three species do not usually mast synchronously suggests, though, that they probably do not form interspecific connections as predicted by Graham and Bormann (1966).

Role of environmental stochasticity

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

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

the P dynamics is maintained medium-term. An economy of scale which itself involves a mechanism for P distribution would facilitate masting when based on storage and thresholds of that same resource. In this respect, ectomycorrhizal networks, which enable P acquisition and uptake (and possibly P storage), could bring about an equilibration of P across the connected roots of neighbouring trees, which would allow a contemporaneous storing and triggering of mast fruiting, as P levels rose in concert across all trees in the population (Fig. 5). In the case of *M. bisulcata* in this study, the key climate variables vary in a somewhat normal way, and it is unlikely they can cue masting in a simple directly linear manner. However, if wetter dry seasons lead to non-linear increases, or pulses, of P-and/or K-uptake, coordinated across the forest, synchrony is also possible. The network idea would also explain why one or both *Tetraberlinia* species often mast fruit along with *M. bisulcata*, because they largely share the same mycorrhizal species (Newbery et al. 1988; Newbery et al. 2000). The non-stationary aspect of the main hypothesis suggests a finely tuned evolved ecophysiological system in *M. bisulcata* allowing it to respond to variation of the climate in order to maximize its fitness.

CONCLUSIONS

The results in this paper confirm and extend the findings based on those for 1989–2004 presented in the Newbery et al. (2006a) with greater statistical detail and confidence. It would have been valuable to know whether the 3-year cycle returned after 2017. Post-dispersal predation is currently important, especially in well-lighted gaps although not in the shaded understorey or below *M. bisulcata* crowns. It could have been much more common in the past when either *M. bisulcata* individuals were scattered across the landscape (Newbery and Gartlan 1996), or when grove dynamics was at the rebuilding stage (Newbery et al. 2013).

1779 Since, seeds and seedlings need P to establish and reach to the network of ectomycorrhizas, it
1780 would be evolutionarily advantageous for an ectomycorrhizal species to mast fruit and
1781 increase its chances of establishment. It is interesting that masting is achieved in the most
1782 clustered caesalps and was not apparent for the more spatially dispersed species in southern
1783 Korup.

1784 Most of the C dynamics models for trees to date (e.g. Cannell and Dewar 1994;
1785 Lacointe 2000; Makela et al. 2008; Franklin et al. 2012) do not cater adequately, if at all, for
1786 environmental stochasticity or non-constant reproductive allocation schedules. Source-sink
1787 models for herbaceous plants, let alone for more complicated trees, have made little
1788 conceptual progress in the last three decades since Farrar (1993), Kozlowski (1971, 1992),
1789 Minchin and Thorpe (1996), and Wardlaw (1990), apart from raising an unresolved debate
1790 over passive versus active storage. They usually assume steady-state equilibrium conditions,
1791 are often teleonomic (e.g. Thornley and Parsons 2014), and are strongly focussed on stem
1792 diameter growth and maximizing tree yield. They are, therefore, still too far away from an
1793 understanding of trees in natural forest ecosystems (Le Roux et al. 2001) to explain even
1794 reproductive schedules like masting. Source-sink relationships, within trees especially, turns
1795 out to be very complicated: a more integrated systems approach is probably required. An
1796 considerable challenge is working out how P, K and N interact with C dynamics over the
1797 complete life-history schedule of a tree. A very interesting hypothesis coming from this
1798 extended phenological analysis is that both K and P levels might synergistically control mast
1799 fruiting of *M. bisulcata*, mediated by the physical structure and functioning of the surface
1800 root mat for nutrient cycling. To test this hypothesis further requires much more detailed
1801 recording of nutrient processes at the tree-level and within the system, replicated over several
1802 mast fruiting events.

1803 The literature review of the likely mechanisms lying behind mast fruiting in *M.*
1804 *bisulcata* gives valuable pointers to detailed aspects that need investigation. The most critical
1805 data for the nutrient resource limitation hypothesis would be phosphorus concentrations in
1806 roots, branches, leaves and fruits of a large sample of trees over several masting cycles.
1807 Detection of phytic acid in branch wood, prior to fruiting especially, could confirm that P was
1808 being stored. Lack of predicted changes in P over time would falsify the hypothesis. In
1809 addition, to test the related economy-of-scale mechanism for equilibration of P between adult
1810 trees at masting would require showing everywhere a flux of P through the mycelia of the
1811 shared ectomycorrhizal network, i.e. between neighbouring large trees.

1812 The fundamental driving variable behind the deterministic mechanically intricate
1813 system operating to cause mast fruiting in *M. bisulcata*, is the stochastic variation in rainfall
1814 (Fig. 5). The vicissitudes of rainfall in the dry season over successive years could generate
1815 the non-linear differences needed to enable the storage process. Stochasticity becomes the
1816 ultimate 'causal' factor over evolutionary time. This can operate at Korup because P as a
1817 resource is strongly limiting the system, there is seasonality, and rainfall alters access,
1818 availability and uptake of P. The hypothesis argues for a fruiting-rooting trade-off as the basis
1819 to alternate bearing and masting. For a common nutrient threshold to operate trees must be
1820 spatially close and connected via their roots and mycorrhizas. The new evidence and analyses
1821 here, showing that both climate and ectomycorrhizas might operate respectively on and
1822 within the forest nutrient cycle, makes for a major step forward in refining the original
1823 PACER hypothesis (Newbery et al. 1997).

1824

1825 ACKNOWLEDGEMENTS

The Ministries of Forests and Wildlife (MINFOF) and Scientific Research and Innovation (MINRESI) granted permission to conduct field research, and the Conservator's Office of Korup National Park approved access to the field site. We thank Sylvanos Ngibili (phenological recording) and Marlise Zimmermann (chemical analysis of plant and soil materials), both of late, for their valuable assistance. Xander van der Burgt helped with the soil moisture readings.

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Supporting information

Suppl. material 1. Radiometry at Bulu, Ndian: calibration and interpretation.

Suppl. material 2. Evidence table for the levels of mast fruiting per year.

Suppl. material 3. Time series analysis of dry season climate variables.

Suppl. material 4. Regression model fits of masting on rainfall and radiation.

Suppl. material 5. Rainfall and 30-day rainfall totals defining dry seasons.

Suppl. material 6. Description and feeding of the yellow-green caterpillar.

Suppl. material 7. Analysis of Ndian PAMOL oil-palm plantation yields.

Suppl. material 8. Stem increments from tree stem cores.

Table 1. Incidence of mast fruiting in *Microberlina bisulcata* at Korup for the years 2005 through 2017, and dry-season climate variables (i.e., last dry season before the event)**.** 'Year/dry season' denotes, for example, the dry season from end 2004 into early 2005, coming before the masting in 2005. 'M' indicates a strong pronounced masting, 'm' a modest but still significant one. This table is a direct continuation of Table 1 in Newbery et al. (2006a) for 1988–89 to 2003–04. The exception to note is the updated radiometer calibration equation applied (Suppl. material 1) which changed the scale (linearly) for radiation. The new radiation values for 1989–2004 are also in Suppl. material 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.

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

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

11 data available. Values from collection years with small superscripted letters (see footnotes) are taken from the earlier studies cited, otherwise the

12 values are newly reported (see Methods).

$t_{>mast}$ (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

13

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

15

16 **Table 3.** Concentrations of the five macro-elements in fallen mature seeds and pods (= fruits) of *M. bisulcata*. Collections were made during the
17 1998 masting event, together with concentrations of the same in mature leaves of this species collected in the same year of a previous (1992)
18 event. Prominent values are shown in boldface. Values with small superscripted letters a – c (see footnotes) are from the earlier studies cited,
19 otherwise the values are newly reported (see Methods).

20

	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

21

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

25

Figure Legends

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

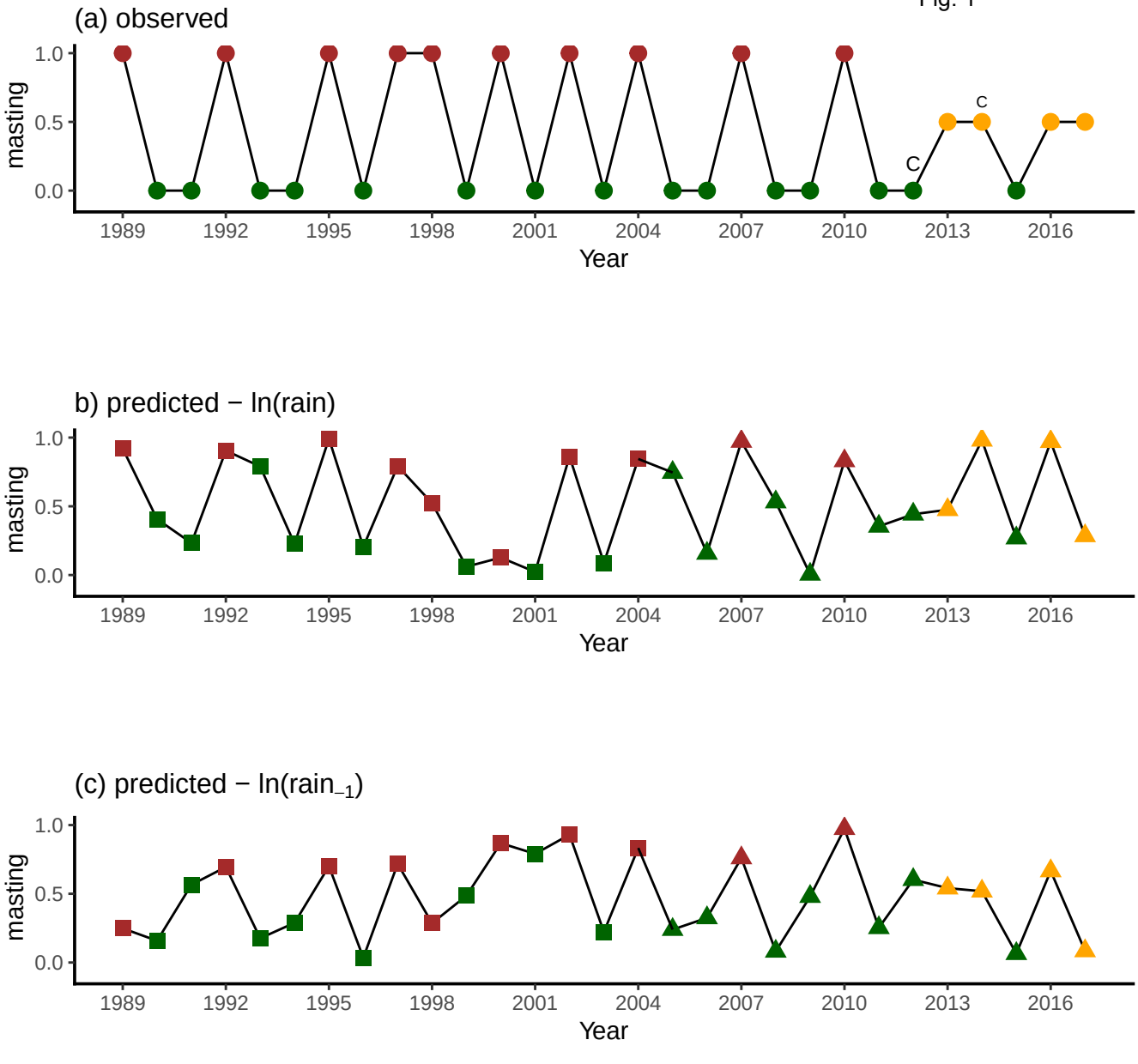
Fig. 2. Times series of the dry season climatic variables associated with the masting series. (a) mean daily rainfall; (b) mean daily radiation; (c) start date (from 1 December of year prior) and (d) duration of the season, i.e. that which preceded the masting event; (e) radiation intensity (= radiation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

Fig. 3. The course of soil moisture content (SMC, %), shown as means and SEs, at (mostly) 40 cm depth, for 2003-2005 at Korup. The horizontal red lines indicate the span of the dry season for each year (see also Suppl. material 5, fig. 1).

Fig. 4. Changes in the mean scores of five phenological stages of *M. bisulcata* trees at Korup in (a) 2009-2010 and (b) 2011-2012. Stages: leaf fall (blue), leaf flush (purple), flowering (green); immature (yellow) and mature (red) pods. The horizontal red lines indicate the span of the dry season for each year (see also Suppl. material 5, fig. 2). Dates of caterpillar attacks indicated with 'C'.

Fig. 5. A schematic flow diagram of the interrelated hypothetical processes behind mast fruiting (M) in the grove-forming population of *Microberlinia bisulcata* at Korup. The boxes with light blue shading are either empirically established in the present study, or at least can be strongly inferred from the literature. They involve the deterministic factors soil phosphorus (P) and potassium (K), and the stochastic effects of dry-season (DS) rainfall; SMC means soil moisture content, and ECM stands for ectomycorrhizal. Those in grey concern radiation and carbon (C)-supply, dynamics and allocation. The box in pale brown-orange concerns the likely important role of ectomycorrhizal networks and nutrient fluxes within the root mat, which are hypothetical and require empirical confirmation. The central double-headed arrow represents the interplay between within-tree and between-tree processes. Green shading and lines indicate the proposed threshold triggering flowering and fruiting, and repeated annual uptake and storage over successive years within the masting cycle of typically 2-3 years. Hormonal control of masting, shown in yellow, is strongly suspected: it also requires critical testing. The small polygon in lilac, centre-left, is the primary condition for mast fruiting to occur, as shown by statistical model fitting in this paper (t is time in years). It is the process-link between the start and end of the diagram. Changes in the degree with which flowering results in fruiting, and in the intensity of fruiting itself (e.g. when lowered to ‘m’), are explained in the main text.

Fig. 1


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

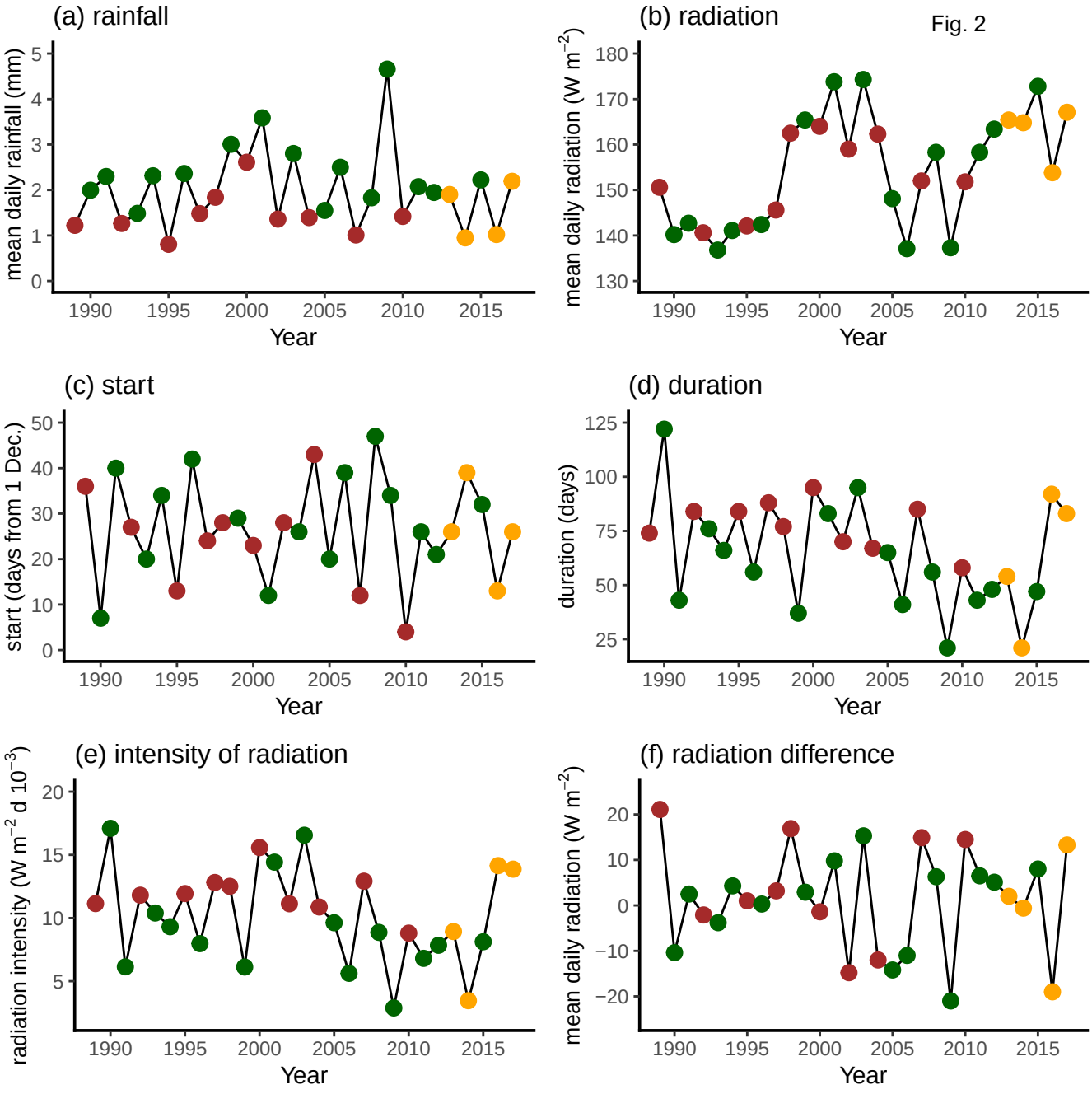
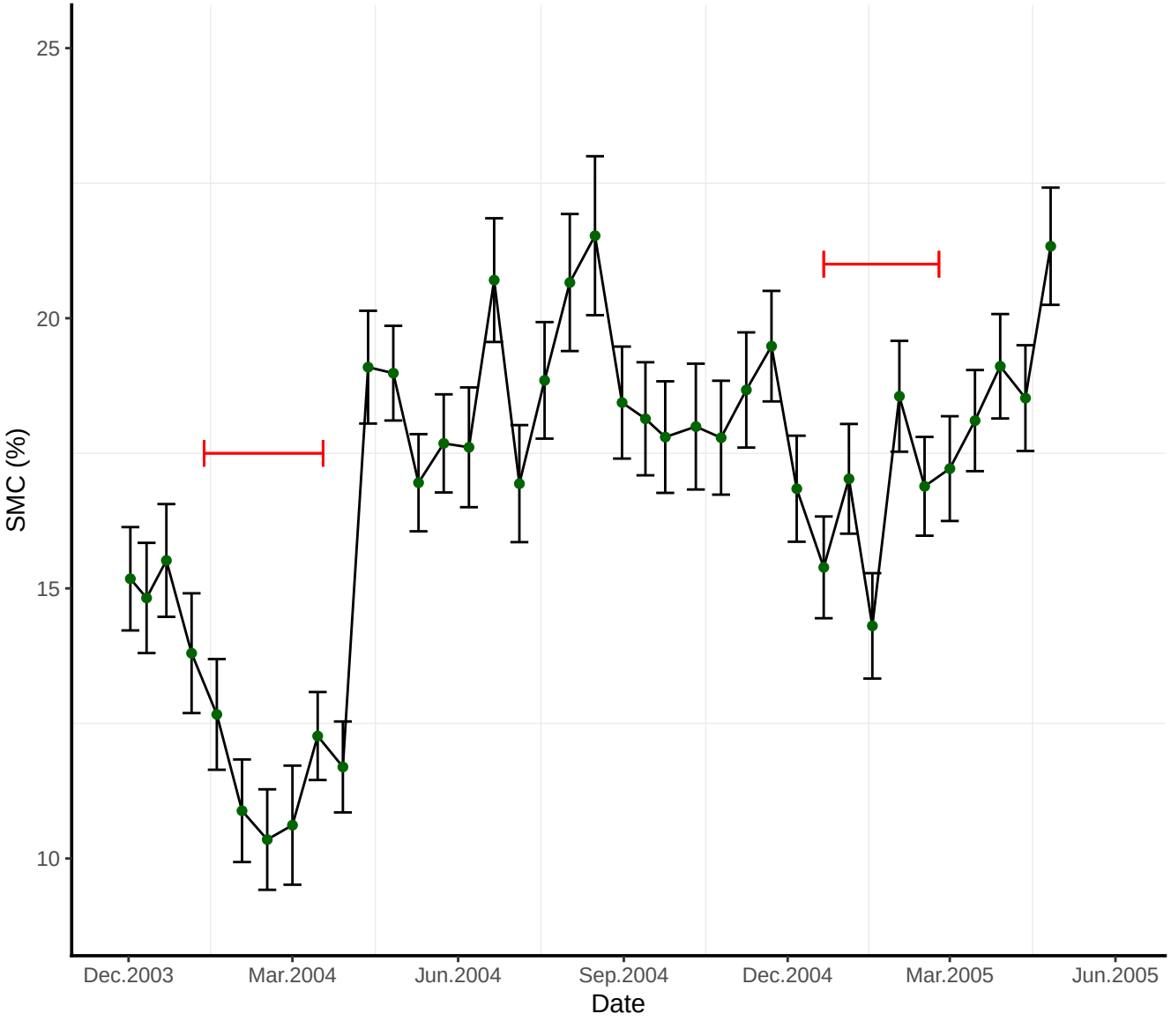

(a) rainfall
mean daily rainfall (mm)
Year
(b) radiation
Fig. 2
mean daily radiation (W m^{-2})
Year
(c) start
start (days from 1 Dec.)
Year
(d) duration
duration (days)
Year
(e) intensity of radiation
radiation intensity (W m^{-2} d 10^{-3})
Year
(f) radiation difference
mean daily radiation (W m^{-2})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

Fig. 3


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

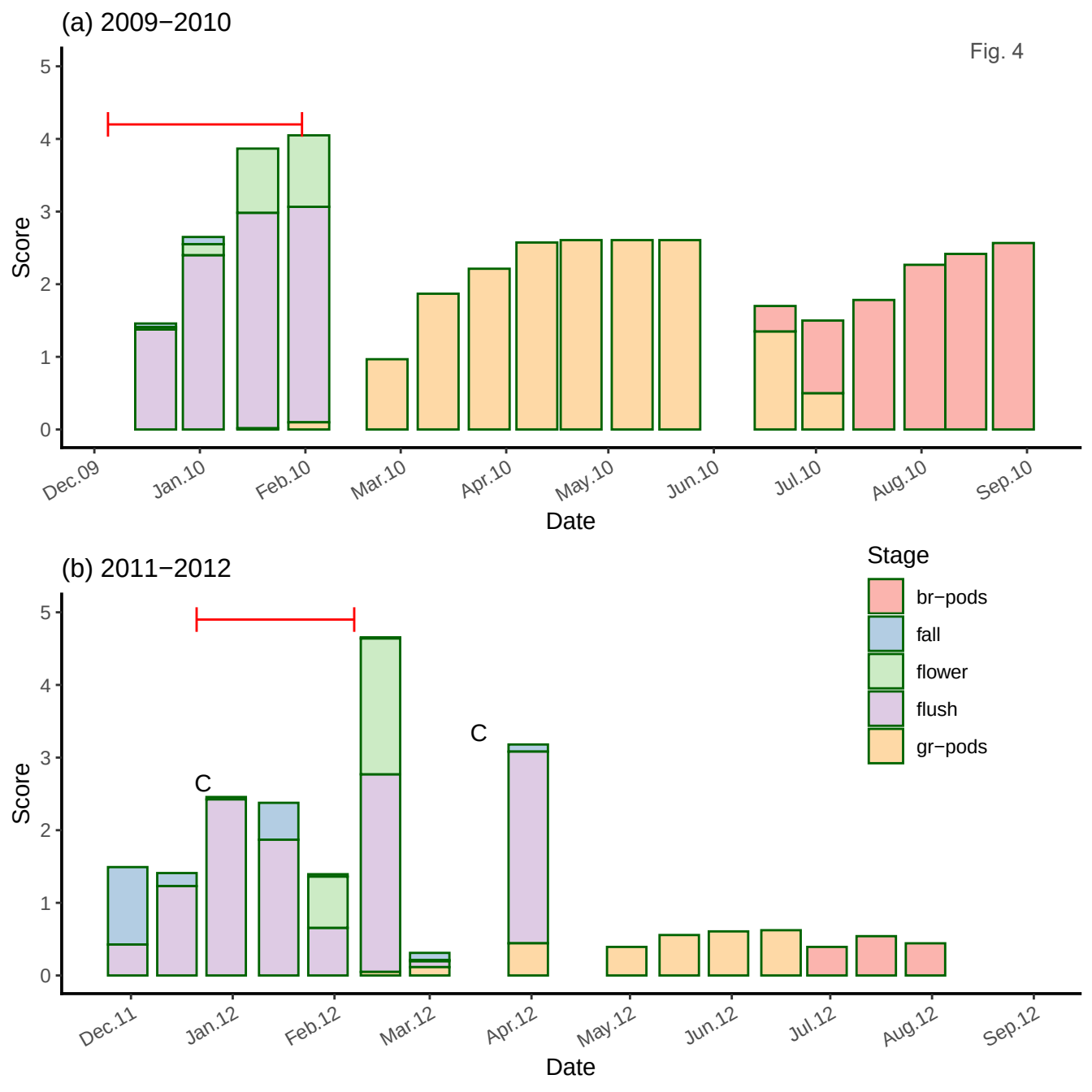
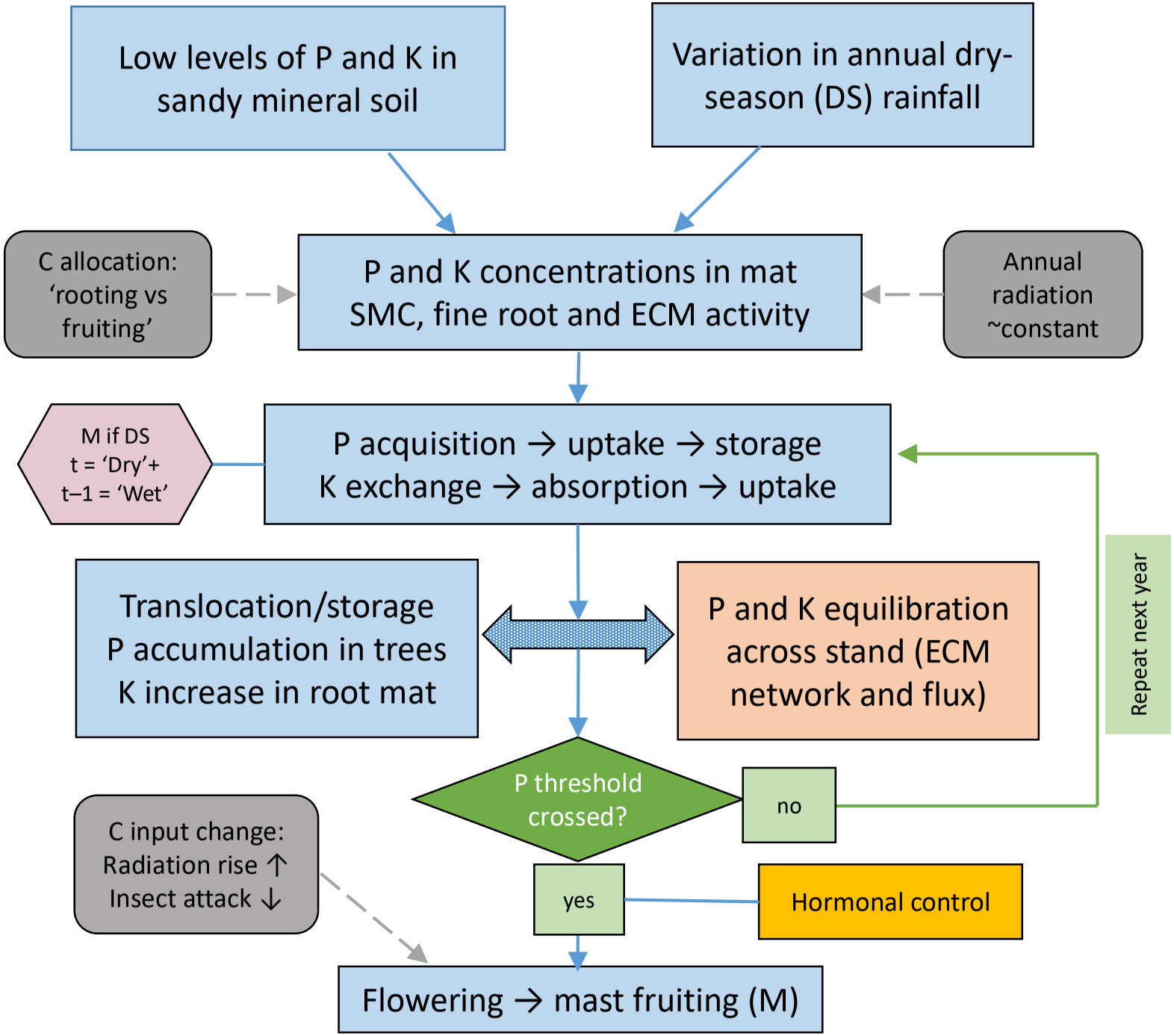

(a) 2009−2010
Fig. 4
Score
0
1
2
3
4
5
Dec.09
Jan.10
Feb.10
Mar.10
Apr.10
May.10
Jun.10
Jul.10
Aug.10
Sep.10
Date
(b) 2011−2012
C
C
Stage
br−pods
fall
flower
flush
gr−pods
Score
0
1
2
3
4
5
Dec.11
Jan.12
Feb.12
Mar.12
Apr.12
May.12
Jun.12
Jul.12
Aug.12
Sep.12
Date

Fig. 5


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