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

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Last updated: 24 January 2024

Abstract

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

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

INTRODUCTION

By fruiting and seeding intensively at intervals as opposed to continuously over the years, seed and seedling survival may be enhanced for plants species with a masting iteroparous type of life-history (Charlesworth 1980, Stearns 1992). Trees provide the large majority of the documented cases. To explain how a species' fitness can be maintained or increased, a so-called 'economy of scale' concept has often been invoked. Three general processes have been proposed to achieve this economy, usually thought of as the teleonomic causes of mast fruiting and seeding: (1) the efficacy of fertilization may be increased by mass flowering, (2) seed predation may be more readily satiated by mass seeding, and (3) the chances of successful dispersal and establishment may be improved by larger reproductive output. The three processes are not mutually exclusive, they can happen together to different degrees and different times, and they could involve non-linear interactions. A model of an evolutionary stable strategy (*sensu* Maynard Smith 1972) for masting appears not to have been worked out so far: a suitable conceptual starting point could be the hypothesis of a serial adjustment of reproductive investment of Lloyd (1980). Stochastic variation in weather conditions from year-to-year, interacting with site substrate conditions, very likely also play important moderating roles in masting.

Kelly (1994), Kelly and Sork (2002), Crone and Rapp (2014) and Pearse et al. (2016) provide reviews of the now extensive literature on mast fruiting, covering many of the key concepts and hypotheses put forward. Much of the reported research has been in the

ecological and evolutionary direction with a strong temperate-biome emphasis however. (e.g. Koenig and Knops 2000). Apart from the dipterocarps in SE Asia (e.g. Curran and Leighton 2000), other studies of masting in the tropics have been very few (although see Norden et al. 2007). More critical is that there still remains a basic lack of understanding of the underlying tree physiological mechanisms which enable mast fruiting and seeding to operate within an ecosystem. Together with the relevant environmental conditions, these mechanisms are sometimes referred to as proximate causes. What are viewed as proximate causes might in fact be the teleonomic ones as well.

For flower, fruit and seed production during a masting year to be allocated efficiently over the life-time of the adult tree, a physiological resource-mechanism must at least be in place. Budget models initiated by Isagi et al. (1997) have simulated how a resource, usually carbon (C), accumulates in storage to an internal plant threshold which then triggers flowering. Almost all such models have involved the coupled wind pollination of individuals (Abe et al. 2016, Satake and Bjornstad 2008, Vacchiano et al. 2018, Venner et al. 2016, Yamauchi 1996, Ye and Sakai 2016). This presents a restricted focus on the Moran effect. There may be more than one mechanism operating over time, or conceivably a mechanism changes in its functioning with ontogeny, depending on site and environment. Further, more than one resource might also be involved, affected by, and effecting, one or more plant hormones that control the cues and triggers which change a leafing axil into a flowering one, followed by fruit maturity (see Marshall and Grace 1992). The individual tree is also probably best viewed as an integrated and dynamic system with regard to the intensity and timing of reproductive allocation. To move forward, more knowledge is clearly needed about the fundamental *modus operandi* behind mast fruiting. Exact mechanisms though can be expected to differ between species, forest types and biomes, each achieving an evolutionary stable strategy via different routes.

The evidence for C as the main resource directly involved in masting is weak. It comes from direct measurements of field trees, manipulations to branches on them in experimental ways, or alternative branch allocations; and from overall C budgets or studies on non-structural carbohydrates (NSCs) and their dynamics (Bustan 2011, Hoch 2005, Hoch et al. 2003, Ichie et al. 2013, Igarashi et al. 2019, Millard et al. 2007, Miyazaki 2013; Mund et al. 2010, 2020; Richardson et al. 2013, Sanchez-Humanes et al. 2011, Würth et al. 2005). Macronutrients have been suggested as potential key resources underlying budget mechanisms from just a few studies, but the evidence is scarce because this topic has been so little researched. Han et al. (2014) and Han and Kabeya (2017), for example, have shown that nitrogen (N) storage and mobilization is important for triggering flowering. Fernandez-Martinez et al. (2017b) and Le Roncé et al. (2023) have indicated that P and Zn, and N and Zn, respectively are likely involved in the mast fruiting of temperate forests. Carbon however should not be laid aside completely as a candidate resource as it usually operates in concert with N, phosphorus (P), potassium (K), and other elements, not just to build fruits and seeds but indirectly for growth and maintenance of other organs like roots for nutrient acquisition.

If macronutrients are behind the mechanisms of mast fruiting it would be expected that the element most important in control might be the one which is at lowest level of availability at the site, being that in most critical supply overall (Allen et al. 2017, Fernandez-Martinez et al. 2019). It will need to be accumulated to support reproduction, which in turn depends of attaining the necessary stoichiometric ratios for seed filling, and doing so without undue costs to other tree growth and maintenance demands in the short-to-medium term. In this way natural selection would be expected to evolve a cueing-threshold-triggering system using this nutrient as a cell storage product. Other elements being in not quite so low supplies, suggests a nested system of storage and thresholds with a similar structure. Even so, the particular nutrients are probably different for different species, habitats and ecosystems.

The search is for the key element(s) most determining growth rate of the trees and controlling nutrient cycling, which then explains the frequency and intensity of reproduction in each situation.

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

The primary hypothesis of the present paper is that limiting mineral nutrients can determine mast fruiting at the mechanistic, tree-physiological and proximate level, particularly in those species that are ectomycorrhizal. This limitation is expected to be strongest where soil mineral nutrients at a site are in critically low supply. Ectomycorrhizas (ECMs) might, hypothetically, also achieve a form of 'economy of scale' due to extensively shared mycorrhizal networks between the roots of large adult trees, which could equilibrate the levels of the limiting nutrient resource (Newbery et al. 1998). Both the tropical Caesalpinioideae-Fabaceae and Dipterocarpaceae are often ectomycorrhizal and commonly show mast fruiting; and among the temperate families (Fagaceae and Pinaceae especially) there is a strong association too between masting and having this symbiotic mode of nutrient

uptake (Newbery 2005). Nevertheless, apart from the review of Corrales et al. (2018), the role of ECMs seem to have been largely overlooked in recent discussions of the causes of mast fruiting (for instance, Pearse et al. 2016).

A secondary hypothesis is that relatively more C should be allocated to other tree parts in the interval years between mast fruitings than years with events. C will assist in nutrient acquisition in the case of roots, and in building new wood and bark storage cells in the case of stems and branches, to allow uptake and storage in preparation for the next masting. With large dry mass allocations during masting events, C is certainly involved. But C may not necessarily be the directly limiting resource for reproduction (Kozlowski 1971).

An ecosystem that might test the nutrient resource limitation hypothesis best would be high-stature primary forest on soils low in one or two elements, e.g. P and K, together with the supporting knowledge of focus tree growth, forest dynamics, nutrient cycling, soils and climate. Such an opportunity is offered by the long-term work in Korup National Park. 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).

Different sets of contingent factors influence the reproductive phenology of different species in importantly different ways. It is therefore essential to understand the site, its forest structure and dynamics, the test species' ecology, and climate variables in some detail first. The processes involved are closely interdependent as a system. The information is laid out in the following 'Background' section. It comes from our long-term work at Korup starting in the late 1970's and it focuses on this particular ecosystem and the hypotheses of the present paper. Later, in the 'Discussion' section, a synthesis of the new results and review of the literature are presented in an interwoven manner. Discussion will very largely concentrate on the role of mineral nutrients in mast fruiting and a new explanatory model for masting.

BACKGROUND

Forest ecosystem

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

The Korup-Ndian area along with Douala at the coast is climatologically special for western Central Africa because it has one clear dry season each year as opposed to the two less-distinct ones found elsewhere in the region. Site elevation is c. 80 m a.s.l. (range 50 to 100 m south to north inland), slightly varying between swampy stream-fed lower areas up to local slopes, in places strewn with quartzite rocks. The soils are very sandy and free-draining,

190 acidic and very low in available P and K (Gartlan et al. 1986), meaning that here high-stature
191 tropical forest is growing on one of the nutrient-poorest sites in tropical Africa. Within
192 groves, soil organic matter is largely confined to the top 2 cm of the profile, forming a
193 surface mat that is densely occupied by fine roots and mycorrhizal hyphae (Newbery et al.
194 1988, 1997). Larger vertical roots are able to tap deeper water reserves. Nutrient cycling in
195 the groves shows a 'fast-forward' modus: leaf litter decay is fast, there is no permanent leaf
196 litter layer, and most cycling via the very efficient mat happens in the early wet season
197 (Chuyong et al. 2000, 2002). At this time throughfall nutrients help to prime decomposition
198 and uptake (Chuyong et al. 2004). For the rest of the year, heavy rains leach the forest, and
199 this results in a tight closed ecosystem in which ECMs play a central role in P acquisition and
200 uptake (Newbery et al. 1997). In addition, annually in the dry season, Harmattan dusts bring
201 some P to the forest by aerial deposition. A critical field experiment showed that growth and
202 recruitment of *M. bisulcata* was not P-limited (Newbery et al. 2002), presumably because of
203 the highly evolved adaptations to the low-phosphorus site.

204 Recruitment of *M. bisulcata* over at least the last six decades has been poor due to
205 very low seedling and sapling survival (Newbery et al. 1998, 2000, 2006b, 2010; Norghauer
206 and Newbery 2010). Seed production in mast years is copious (Newbery et al. 2006a) but this
207 species' seedlings are strongly shade-intolerant (Green and Newbery 2001a, b). The groves
208 demonstrate transient dominance: the stands now are predominantly made up of large to very
209 large trees, with extremely few small ones present (Newbery et al. 2013). The dynamics is
210 thought to be one of patches arising and then decaying, being replaced, *in situ* or *ex situ*,
211 within a mosaic of species-richer forest (Newbery et al. 2013, Newbery and Gartlan 1996).
212 The species is classified as a long-lived light-demanding tree (see Newbery et al. 2010). Part
213 of the expected life-history strategy of long-lived and light responsive species such as *M.*
214 *bisulcata* (Newbery et al. 2010) would be to delay the size on maturity (SOM) in order that

215 greater seed output later offsets the relatively low probability of persistence in the forest
216 understorey. Two further coevolved traits are ectomycorrhizal habit and mast fruiting.
217 Ectomycorrhizas not only provide advantages in resource acquisition for juvenile and young
218 adult trees but are also thought to be a means to store resources which enable mast fruiting in
219 the older adult ones (Newbery et al. 1998; Newbery et al. 2006a). A key sub-hypothesis is
220 that these links, and possibly also root grafts, between adults synchronize the timing of masts
221 by equilibrating nutrient sinks across groves (Newbery et al. 2000, 2010). There is increasing
222 evidence from other forests that ectomycorrhizas build intricate below-ground hyphal
223 networks between individual trees (e.g. Simard et al. 2012, Simard and Durall 2004),
224 although the definite evidence for these networks providing a means of C or mineral nutrient
225 transfer is not consistent, at least for adults to seedlings (Karst et al. 2022). However, in the
226 context of mast fruiting of adults, the hypothesized transfers are between very large trees
227 occurring in dense stands (the groves at Korup).

228 *Mast fruiting*

229 Mast fruiting in *M. bisulcata* was first realized from early phenological recording in
230 1988 to 1995, with prominent seed crops in 1989, 1992 and 1995 and barely any seed fall in
231 the intervening years (Newbery et al. 1998). Flowering occurs to some extent in most years (a
232 few fail completely); and not always does a heavy seed crop depend on heavy flowering
233 (Newbery et al. 2006a). The two *Tetraberlinia* species tend to mast in the same years as *M.*
234 *bisulcata* but not both together (Newbery et al. 1998, and unpubl. data). After a propitious
235 start with a potential 3-year cycle for masting (i.e. a 2-year interval between mast years), this
236 cycle turned out to be shorter in the longer term. Because masting was associated with peaks
237 in mean daily radiation in the dry season prior to fruiting this suggested that C was at a
238 premium, and some threshold needed to be crossed before masting occurred. Detailed
239 nutrient cycling studies in plots dominated by *M. bisulcata* showed for the first time that leaf

240 litter after a mast year (1989) was low in P concentration compared with the years to either
241 side, and this was matched by a decline available P in the soil, especially in the surface
242 organic layer (Newbery et al. 1997). This last result suggested that P was being shunted into
243 the seed crop and less was remaining to be shed in litter, and given the low soil P at the site
244 and the presence of ECMs, P was also likely limiting mast fruiting. Tree C and P levels might
245 be operating a double-threshold control system and this led to the phosphorus and climate
246 ectomycorrhizal response (PACER) hypothesis proposed by (Newbery et al. 1997).

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

265 substantial allocation of resources (Green and Newbery 2002). Seeds and pods together had
266 N and P amounts 13 and 21% of that in annual leaf litter production, indicating an important
267 use of P during masting. Unfortunately, C, P, N and K investments in flowers are unknown
268 but if included they would increase the reproductive allocation estimates slightly. Flowers of
269 *Microberlinia* are very small in mass compared with seeds and fruits.

270 Using a detailed 150-tree phenological study in the main P-plot at Korup of 1995-
271 2000, and incorporating circumstantial reliable observations in the field from previous and
272 later years up to 2004, enabled a better picture of how dry season variability might control
273 mast fruiting in *M. bisulcata* (Newbery et al. 2006a). From daily rainfall and radiation data
274 (recorded locally at Bulu, Ndian; 1984-2017), a clearer model was developed. Masting was
275 tending to occur when the prior dry season was *more* intense than average (low mean daily
276 rainfall), plus the dry season in the year prior was *less* intense than average (high mean daily
277 rainfall). After 1993, radiation did not show the same trend as in 1989-1992, largely because
278 after 1995 it climbed steeply as part of an inferred 11-year solar cycle (Newbery et al. 2006a).
279 What was perhaps important was the relative change in radiation between successive years
280 and not the absolute levels. The notion that time series of the environmental variables at
281 Korup were or ever had been stationary is hard to sustain.

282 The argument developed was that the current year's dry season dryness reflected also
283 to some degree increased radiation, but the wetter dry season the year prior was possibly
284 indicating better conditions promoting tree nutrient uptake at the most effective time. The
285 detailed phenology data showed that masting was strongest on trees on upper slopes (i.e. sites
286 with relatively drier surface soils in years with a 'dry' dry-season), and that in the moderately
287 'wet' dry season of 2000, those trees that masted were also on the drier sites. This tentatively
288 pointed to surface soil moisture in the dry season being a key determinant to what was
289 happening. The intensity of the dry season is unlikely to have particularly affected the water

290 balance of adult trees themselves because they would have had access to deeper water
291 sources: after all, trees flushed, leaves and branches grew, and flowering took place, in the
292 dry season. Taken together, the preliminary evidence pointed to processes in the organic mat
293 regarding fine roots and ECMs, coupled to nutrient transfers within the trees and
294 ectomycorrhizal network (Newbery 2005, Newbery et al. 2006a). With the masting time
295 series extended to 29 years—almost twice its previous length, plus information collated from
296 several nutrient studies at the site, further tree phenology censuses, a more detailed statistical
297 modelling of fruiting on rainfall and radiation, and the effects of an unexpected herbivore
298 attack—this paper assesses the extent to which C, P and K, might be determining the masting
299 cycle in *M. bisulcata* and, *in extensio*, presents a more refined hypothesis and model of this
300 remarkable phenomenon.

301

302 METHODS

303 *Location*

304 Korup National Park, in the South-West Region of Cameroon, is covered by primary
305 rain forest of the Atlantic Coastal type (Letouzey 1968), and lies within the Guinea-
306 Congolean refugium (Gartlan 1992). Phenological recordings were made in the main 'P-plot'
307 located in the southern part of the Park (5º10' N, 8º70' E) at an elevation of c. 100 m a.s.l.
308 (see Newbery et al. 2004, 2013). Mean rainfall 1984-2016 was 5159 mm (range 4023 to
309 6531). Access to the neighbouring oil palm estates of PAMOL Plc outside of the Park (Bulu-
310 Mundemba, Ndian) allowed a comparison of their fruit yield with *M. bisulcata* mast fruiting
311 with regard to climate variation. The estates have the same substrate and soil type as southern
312 Korup. After initial trials in the 1960s through to the late 1970s, phosphate fertilization was
313 discontinued because little beneficial effect on palm nut production was found (C. E. Etta,
314 PAMOL; unpubl. data).

Climate

Climate data continued to be available from the PAMOL Bulu Station, Ndian (Etta et al. 2022). The station lies 12 km to the SE of the study site. Daily radiation, rainfall and temperature were recorded since 1 January 1988 until 27 May 2017. Radiation was estimated using a Gunn-Bellani (BG) radiometer, with volume evaporated per day (V, ml) convertible into radiation (R, W m^{-2}). Two periods, however, lacked radiation data because of instrument failure in March-May 1993 and April 2009 - May 2011. Improved new radiometer calibration equations were developed using several shorter series of pyrometer measurements and these applied to the complete time series to obtain mean monthly radiation (Appendix 1). The short break in radiometer readings had been previously linearly interpolated, but the radiometer data for the much longer break 2009-2011 required more refined statistical methods. These are outlined in Appendix 1. Since radiometers are rarely still in use today, this step in methodology is original. It also meant that the standard BG instrument calibration curve (used in Newbery et al. 2006a) could be replaced with the now much better site-specific parameters. The equations were applied to the whole series 1989-2017, with differences to the first half of the series referenced in Appendix 1. World Climate data bases unfortunately proved quite inadequate for estimating these missing values due to the sparseness of regional stations in western Central Africa, the special topography around Mt. Cameroon, SSE of Korup, with the few data records available for the last decades being incomplete (see Appendix 1).

A dry season occurred when the 30-day running rainfall total (*rft*) at Ndian (Korup) was < 100 mm, and this gave a defined start date and duration (the 'drought-defined dry season' of Newbery et al. 2006a); This dry season typically moved one month back or forward around the modal months of December to February, coming earlier or later in different years, and being shorter or longer. Hence, in what follows, 'dry season 1991' for

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

350 *Phenology*

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

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

364 fall, leaf flush, flowering and immature and mature pods (scale 0-3; Newbery et al. 2006a).
365 Later, now within an 8-ha sub-area of the 82.5-ha P-plot (1000-1200 m E, and 100-500 N,
366 with respect to SW origin; see Fig. 2a of Newbery et al. 2013), 61 of the 65 trees surviving
367 since the last enumeration in 2005 (stem diameter, mean ± SE = 112 ± 4 cm, range = 54 –
368 174 cm), were scored between 2009 and 2013 in a similar manner as the first period. In 2014,
369 fallen pod density on the ground was taken as a proxy for mature pod density (Appendix 2,
370 Table S1). Direct estimates of seed output as a quantitative measure of mast fruiting, or even
371 qualitative crown scoring, on trees in all years was simply not feasible at this remote and
372 difficult field location in Korup.

373 *Nutrients*

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

389 averaged across the three constituent months. A mast fruiting occurred in (August-
390 September) 1989, so dry season 1990-1991 is the second dry season after the event, and dry
391 season 1991-1992 the third one. The next masting was in the wet season of 1992, so seen
392 from this perspective the two dry seasons sampled were ~ 6 and 18 months prior to the
393 second event.

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

407 In the dry season 1997-98 four traps of galvanized metal (same as used in 1990-92)
408 were compared with four similar ones but with hessian sack linings (used in the 1989-1991
409 study of Newbery et al. 1997), each set being placed at random in each of the two quarter
410 plots of six HEM half-plots. Litter was collected over four consecutive fortnights between 21
411 December 1997 to 15 February 1998. *Microberlinia bisulcata* leaflets and rachises were
412 again sampled separately, dried and analyzed for N and P concentrations. Not all traps had
413 sufficient material and the replication per subplot/trap type/date ranged from 2 to 4. N and P

414 values were successive averaged for trap type, then subplot, and their weighted 4:1 leaflet-
415 rachis averages found for the 24 date x plot combinations. Trap type had no effect on these
416 two elements' litter concentrations (testing for Zn contamination had been otherwise
417 intended). This litterfall was collected midway between a moderate double masting in wet
418 seasons 1997 and 1998.

419 The 1998 masting event's seeds and pods, previously analyzed and reported in Green
420 and Newbery (2002) for N and P, were analyzed further for K, Mg and Ca using standard
421 acid digest methods and spectrometric determination (see e.g. Newbery and Neba 2019). To
422 find the nutrient masses allocated to reproduction (fruits) and to compare them to the same
423 used in foliage, seed and pod densities, together with leaf litterfall in another similarly strong
424 (1992) mast year, were taken from Green and Newbery (2002). In these new calculations,
425 mature leaf concentrations (for N and P) were used from a retranslocation study in Chuyong
426 et al. (2000), which involved three dates: viz. December 1991, and April and July 1992. Litter
427 fall dry mass would have been very slightly underestimating mature leaf mass because of
428 some element retranslocation during senescence. Essentially, these leaf concentrations were
429 from trees sampled on average 5 months before seed dispersal, and therefore concurrent with
430 pod maturity that year.

431 In a separate study of litterfall by Schwan (2003), paired litter traps (same again as
432 used by Chuyong et al. 2000) were placed at random below the crowns of 20 *M. bisulcata*
433 trees in the main P-plot. The bulk of the litter (~90%) fell in the 3-week period of 9-30
434 December 2002. This 2002-03 dry season came immediately after a masting in 2002, and
435 next one was in 2004 (Newbery et al. 2006a). In this study only leaflets were analyzed for N,
436 P, K and Mg.

437

Soil moisture

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

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

RESULTS

Mast fruiting cycle

The extended time series shows that after 1995 there was a double year 1997-98 with high seed crops, 1998 somewhat weaker than 1997, and then the interval dropped to 1 year (from a 3- to a 2-year cycle), with a masting sequence 2000, 2002, and 2004, returned to very strong masts in 2007 and 2010 with a 2-year interval, and then after that the control seemingly weakened to result in two pairs of consecutive years, 2013-14 and 2016-17 which

462 had moderate masting fruiting (Fig. 1a). The time series as it extended began to show
463 increased non-stationarity, the first-detected period of 3-year cycling of 1989-1995 returned
464 only once in 2004-2010: the regular cycle was seemingly just temporarily disturbed.
465 Nevertheless, 'on average' over the 29 years, and taking as markers the first of those pairs of
466 years with partial masting (2013, 2016), there appears to be good evidence of an intrinsic 3-
467 year cycle. Because the time series is evidently non-stationary, any tests of randomization
468 using techniques such as bootstrapping will not provide valid inferences (Cox 1981).
469 Furthermore, bimodality will not be detected if the interval varies between 0 and 2 years.

470 The fitting of masting, as a 0/1 binomial response variable, to the climate variables
471 was first limited to the 24-year period 1989-2012 because all the events were strong and
472 pronounced ('M' in Table 1; Appendix 2, Table S1). After 2012 there appeared a new
473 'regime' of two sets of two consecutive years which showed only moderately strong ('m')
474 masting. Logistic regressions were run with dispersion (φ) either fixed at 1.0 or allowed to be
475 estimated (Agresti 2007). Whilst the latter gave marginally more significant fits, the former
476 was adopted because the sample size was small and the estimation of φ would be unreliable
477 (McCulloch and Nelder 1989). The models were therefore parsimonious and quite
478 conservative with regard to Type I errors. Tree responses in each year were doubtless not
479 fully independent from those 1 or 2 years before, being part of the inherent process of mast
480 fruiting: the simple form of logistic regression did not account for temporal autocorrelation.
481 With records for only *c*. 60 trees in common across all events, the sample was not sufficient
482 enough to apply Monte Carlo subsampling to gain temporal independence. An event (masting
483 = 1) was a composite outcome for all trees and, necessarily, it meant that almost all
484 individuals were responding in a similar manner even though there was quite some variation
485 in fruit production among individual trees. Using the binomial scale (ordinal for the last

years) reflected the definiteness of masting in *M. bisulcata.* Over the whole time series, it led to conservative statistical testing of both hypotheses.

Climate variation

Of the four basic climate variables, mean rainfall and radiation per day in the dry season, and start and length of the season (current year of masting and year prior) in Figure 2, only the first required ln-transformation to ensure too an evenness of X-axis spread in values of this independent variable. Extending the analysis to the full 29 years (1989-2017) required using the ordinal, or proportional-odds, logistic model (Agresti 2007, Fox 2008, Hosmer et al. 2013), where 'm' (moderate masting) was scored as 0.5 (see Appendix 2, Table S1). Binomial and ordinal logistic models were run with the 'glm' and 'polr' commands in R (Fox and Weisberg 2019; Venables and Ripley 2002, package 'MASS'; R Core Team 2022), and in GenStat for comparison where also φ could be estimated (VSN International (2022). Given the modest length of the time series and data set, different models were fitted mostly with single independent terms, and when with two then the same variable with a 1-year lag, and only additively. No attempt was made to search for a best-fit subset model with interactions; if fact, most such model fits failed to converge when attempted. The binomial error distribution appeared satisfactory: the complementary log-log one as an alternative did not improve fitting.

Mean daily dry-season rainfall in years of full masting was lower than in those years' prior with no masting (Fig. 2a), with the exception of 2000, and if the averages of the rainfall values for the two double partial masting years are taken these are on a par with the masting ones. The time series for rainfall showed weak temporal autocorrelation (Appendix 3: Fig. S3a), and likewise albeit a little more strongly for ln(*rain*) at lag 1 (–0.293 vs. –0.221). (Note that the first correlation differs slightly from the rain versus $rain_{-1}$ one based on data which

included the lagged 1988-value.) Radiation over time showed a distinctive pattern with a clear central peak between 1996 and 2005, then a rise again, apart from 2009, to those higher levels (Fig. 2b): accordingly, the series evidenced non-stationarity, and as a consequence autocorrelation was positive and significant for lags of 1 and 2 years, then significantly negative ($P < 0.05$) for lags of 6-8 years (Appendix 3: Fig. S3b).

Start of the dry season varied around the third to fourth week of December with no clear patterns or differences between masting and non-masting years (Fig. 2c), but it was negatively autocorrelated with a lag of 1 year, i.e. early starts tended to be followed by late ones, then early again, in successive years (Appendix 3: Fig. S3c). Excepting the two last years, duration of the dry season revealed a general decline (an approximate halving), those years with masting being often longer, and conversely of the six shortest-season years there was no masting, apart from 2014 which was partial (Fig. 2d). Interesting, autocorrelation of duration was almost just significant ($P < 0.05$) at a lag of 3 years (Appendix 3: Fig. S3d). Radiation intensity showed a very similar pattern to duration (since radiation varied much less than duration) (Fig. 2e; Appendix 3: Fig. S3e). Intensity of radiation in the dry season was expressed as mean daily radiation x duration. Lastly difference in radiation ($radi_d$) between successive years (one approach to removing trend) was mixed with regard to masting response, although again a weakly significant negative autocorrelation for a lag of 1 year was evident (Fig. 2f; Appendix 3: Fig. S3f).

Masting and climate

Binomial logistic regressions for 1989-2012 showed a significant negative effect of mean daily rainfall in the current year's dry season ($P < 0.05$), a positive effect of mean daily rainfall in the dry season prior ($P < 0.05$), on masting. Using ln($rain$) and ln($rain_{-1}$) improved the regressions fits with $P < 0.015$ (Appendix 4: Table S1). Mean daily rainfall was only

weakly correlated with rainfall the year prior, untransformed values ($r = –0.190$, $P = 0.374$, transformed ($r = –0.272$, $P = 0.15$). This last result is important because a strong negative temporal autocorrelation, i.e. a year-to-year increase-decrease reversal, was absent. Regressions with both rainfall terms led to reduced fitting, because these coefficients were now partial ones adjusting for the correlation ($P = 0.093$ and 0.055). The same with ln-transformed variables also changed the significance levels very little ($P < 0.10$; Appendix 4: Table S1). Ordinal logistic regressions improved the fitting further with the full 1989-2017 data. Concentrating on the models using ln-transformed variables, separate regressions were now more, and highly, significant ($P < 0.01$), coefficients with the same signs as for the simpler binomial logistic ones (Appendix 4: Table S1 and Fig. S1) and, whilst significance decreased again using two-term models, they were still relatively strongly significant overall ($P < 0.025$).

The mean difference in ln-transformed dry-season mean daily rainfall, ln(*rain*), between the current masting (t_0) and year prior (t_{-1}) was highly significant ($P < 0.005$), but much weaker for the same and penultimate year (t_{-2}) ($P = 0.15$). Back-transformed means were 1.37, 2.49 and 1.69 mm/day respectively (see Appendix 4: Table S2). Comparing rain at t_0 with means of *rain* at t_{-1} and t_{-2}—applying equal or unequal weighting—led to very similar results as those at t_{-1} alone ($P < 0.005$). As a robustness test of the strong vs moderate ('M'/'m')-grading of mast fruiting, and how that might have affected the relationship with mean daily rainfall in the dry season, where there was some uncertainty in the final grading, 1989-2017 ordinal logistic regressions were rerun with the 'M' for 1998 and 2000 replaced by 'm', i.e. 1.0 by 0.5. The dependence of masting on ln(*rain*) in the current and prior seasons became slightly stronger ($t = –3.209$, $P = 0.0036$; $t = 2.913$, $P = 0.0074$, respectively).

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

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

Radiation did show a long-term trend since the start of recording until 2017 (Appendix 3: Fig. S2), with the evident 11-year cycle. This was not related to change in instrumentation at Bulu (Appendix 1). Using a LOWESS regression fitting model in R ('lowess' command—a set of local smoothing splines, this trend could be removed and the differences between empirical measurements and the detrending curve then used as adjusted local year-to-year changes Appendix 3: Fig. S2a). The best result was with a span parameter of $f = 0.25$, which meant that radiation values > 1 year prior or ahead had some weight in fitting values for any one year, which simple differences between successive years did not. Binomial (1989-2012) and ordinal (1989-2017) logistic regression fits of masting to drought-defined dry-season *radi* and $radi_{-1}$ were, however, all clearly insignificant ($P = 0.34$ to 1.00).

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

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

596 *Model predictions*

597 Using binomial logistic regressions of masting 1989-2004 on ln(*rain*) in the current
598 and previous years, fitted models were used to predict masting in 2005-2017 (Fig. 1), on the
599 original response scale of 0 to 1 (π; Agresti 2007). The series started at 1989, not 1987 as
600 used in Newbery et al. (2006a); and autocorrelation was not incorporated (see 'Time series
601 analysis' later though). The model fit for ln(*rain*) was good for the mast years 1989, 1992,
602 1995 and 1997 (marginal for 1998), and good for 2002 and 2004, but it wrongly indicated a
603 mast in 1993 and missed the mast in 2000 (Fig. 1b; fitted intercept [α] = 3.61 ± 1.80 and
604 slope [β] = –5.77 ± 2.62, $t = -2.206$, $P = 0.027$). Predictions of masting in 2007 and 2010
605 were very high ($\pi = 0.97$ and 0.83 respectively), and also that it did not occur in the
606 intervening years. After 2012 though, one each of the pairs of moderate ('m') masts was

predicted as full ('M', $\pi = 0.98$ and 0.97). The predicted masting in 2005 ($\pi = 0.75$) was incorrect, however.

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

The median effective level of ln($rain$), that is the level when π (x) = 0.5 (defined as $x = -\alpha/\beta$; 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 modelling

Times-series logistic regression—in full generalized logistic autoregressive moving-average regression, with the command 'glarma' (R package glarma, Dunsmuir and Scott 2015), that accounts for temporal autocorrelation in binomial data (Cox 1958, 1981; Cox and Snell 1989, Dunsmuir 2016; McKenzie 1985, 2003), 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, (Appendix 4: Table S1). 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 more strong negative effect of duration was evidenced for the year prior ($duration_{-1}$; $\beta = -0.099 \pm 0.038$, $z = -2.62$, $P = 0.0087$) (Appendix 4: Fig. S2). 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), and time-series logistic regression fits

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

Radiation on quarter-year basis

Whilst a rainfall deficit delimitation will define the drought period in terms of limited water availability, it may not necessarily correspond precisely though to heightened radiation as well. Returning to the modal definition of dry season, namely the calendar months December through February (DJF), or first quarter of the phenologically referenced year, mean daily radiation can likewise be found (Appendix 3: Fig. S1a). Masting was not strongly related using binomial, ordinal or time-series logistic regressions, to this quarter's radiation however, in either the current or prior year ($P \geq 0.18$; Appendix 4: Table S3a), and also not for the other three quarters (Appendix 3: Fig. S1b-d; $P > 0.4$; model fits not shown). By contrast, and surprisingly, masting was strongly dependent on the *difference* in radiation, both in absolute ($radi_d$) and percent change ($radi_{d\%}$) terms, from prior to current year, and with all three regression models (P = 0.007 to 0.024; Appendix 4: Table S3a and Fig. S3; Appendix 3: Fig. S1e). Using again lowess smoothing regressions to remove trend in radiation (Appendix 3: Fig. S2b), with binomial logistic regression (1989-2012) masting weakly positively depended on differences in *radi* (P = 0.051), negatively though more marginally for $radi_{-1}$ ($P < 0.1$) (Appendix 4: Table S3b and Fig. S3). Time-series logistic regressions improved the fits especially for *radi* ($P < 0.02$), although only slightly for $radi_{-1}$ (P = 0.80). Fits to detrended differences (1989-2017) with ordinal logistic regression were intermediate in significance to those with binomial and time-series logistic ones (Appendix 4: Table S3b). Overall, there is moderate to strong evidence that the larger the increase in radiation between

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

An interesting feature of the LOWESS fits (Appendix 3: Fig. S2), when taking radiation according to the two definitions of dry season, is how the outliers changed in relation to the smoothed curves. In the drought-defined case, 2001 and 2003 (both 1 year before masting) were very high, and 2006 and 2009 (also both 1 year before masting) were very low. Changing to the DJF-defined case brought 2001 and 2009 radiation much closer to the curve, and the binomial and time-series regression fits were improvements. Further, the autocorrelation was notably stronger, positive and significant, at lags of 1 and 2 years for this DJF-defined dry season than the drought-defined one, shifting to a significant negative correlation at 8 years lag (Appendix 3: Fig. S4a). In the third (JJA) and fourth quarters a similar but slightly weaker pattern for the function occurred, the negative lag now at 10-12 years (Appendix 3: Fig. S4b, c). More interesting, however, was the almost unstructured weak pattern of the function for the second (MAM) quarter, that is no temporal autocorrelation over the early wet seasons (Appendix 3: Fig. S4d).

Start and duration of dry season reconsidered

To shed some light on the apparent paradox of the different definitions of dry season determining the relationship between masting and radiation, regression models were rerun with an extended dry season of the months of November through to March. All binomial logistic model fits, 1989-2012, using radiation in the current and prior dry seasons on this new basis were clearly insignificant (P = 0.27 and 0.69). However, dependence of masting on $radi_d$ was marginally significant at P = 0.071 ($radi_{d\%}$, P = 0.052), and correspondingly so for the time-series logistic model with p = 2 (P = 0.056 and 0.043). Compared with the fits for

the models using DJF as dry season (Appendix 4, Table S2a), these results for the 5-month season are weaker, suggesting that the influence of radiation was being diluted by inclusion of the additional 2 months; and this was reflecting the early wet season autocorrelation. Comparing radiation defined by DJF and that defined by the drought dry season graphically, both for differences between successive years and as residuals from the smoother curve over time (Appendix 4: Fig. S4), indicated that a majority of the years lying above the 1:1 reference line were ones with masting and most of those below were non-masting, attesting *inter alia* that raised radiation differences and deviations were associated with mast fruiting.

The placing of start and end dates of the dry season was evidently critical to the analysis outcome because the degree of overlap between the two types of dry season were very variable from year to year (Table 1, Fig. 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.

Tree size-fruiting relationship

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

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

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

753 at the 20-and 40-cm depths were very small and insignificant: 10.98 vs 10.69% in 2003-04
754 and 16.20 vs 15.89% in 2004-05, $P = 0.88$ and 0.89 respectively, df = 1,10). In a similar-
755 length period in the late wet season 2004, starting soon after the peaked occurrences that
756 year, a small difference was evident but again it was clearly not significant (20.20 vs 18.13%,
757 df = 1, 10; $P = 0.39$). Interactions between depth and time were all insignificant for all three
758 short periods ($P = 0.19$ to 0.36).

759 After the strong dry season of 2003-04, during which SMC reached a minimum of
760 10.4%, its values remained fairly constant at 18.24 ± 0.31%. The dry season of 2004-05 had
761 much less influence on SMC (Fig. 3). The lowest SMC-values in 2004 coincided with the
762 lowest *rft*-values (down to 12 mm then 0 mm over 4 weeks); in 2005 SMC did not go either
763 so low or remain low for long, and the match with SMC was weaker. At the start of the 2003-
764 05 series, the means (± SE) of SMC recorded and those found by gravimetric analysis were
765 15.09 ± 0.52 and 15.50 ± 0.82% respectively. The estimates were positively correlated ($r =$
766 0.677, df = 10, $P = 0.016$). Saturated water holding capacity was on average 38.15 ± 1.16%,
767 less than the SMC at the peak times confirming that the locations were not always free-
768 draining.

769 Between 2 December 2003 and 26 April 2005, SMC was related to 30-day running
770 rainfall total as follows: SMC = 14.4 + 0.0070·rft ($R^2_{adj} = 40.5$ %, $F_{1,36} = 26.18$, $P < 0.001$, n
771 = 38), inferring 14.4 % at 0 mm, and 21.4% at 1000 mm – the last *rft*-value being close to the
772 June 2004 maximum of 995 mm. The difference in SMC between the very driest and wettest
773 times of the mast year was therefore only 7% — for those assumed free-draining locations.
774 SMC before the dry season of 2006-07 was 20.7 ± 0.10%, and declined sharply and almost
775 linearly to 14.0 ± 0.67% ($n = 9$ sensors), a difference of 6.7%. With the dry season that year
776 lying within the span of SMC recording dates, this last value was likely very close, if not at,
777 the 2007 SMC minimum. The mean value at 29 January 2011, a date also well into that

778 year's dry season was 16.2 ± 0.8% (n = 8, one sensor lost because its cable was chewed), a
779 value close to that in the dry season of 2005 (Fig. 3).

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

793 *Caterpillar attacks*

794 Chance attacks by herbivores offer good opportunities to assess how loss of foliage,
795 and hence photosynthetic activity, could interfere with tree reproduction. In the latter half of
796 December 2011, and again in the first half of March 2012, an outbreak of a black caterpillar
797 was observed that fed on young foliage of *M. bisulcata* trees recorded for phenology in the P-
798 plot. Although not quantitatively measured, the attacks were extensive, as evinced by the
799 substantial amounts of falling frass, numerous caterpillars hanging below the crowns on
800 threads, and litterfall consisting of soft, green leaf tissues (G. A. Neba and S. Njibili, pers.
801 obs.). The same caterpillar was also recorded at another *M. bisulcata* grove 4.2 km due south,

802 in March 2012 (Norghauer et al. 2023). However, no visit was made to that site in December
803 2011. Fallen caterpillars were also observed feeding on young leaves of *Oubanguia alata*, a
804 common understorey tree growing below *M. bisulcata* crowns at Korup.

805 Also in the latter half of December, but in 2008, an outbreak of most likely the same
806 caterpillar species (an *Achaea* sp., probably *A. catocaloides*) had been recorded on *T.*
807 *korupensis* trees in the same P-plot (Norghauer et al. 2023). At that time, feeding upon *M.*
808 *bisulcata* foliage was limited to low levels on just those crowns closely adjacent to the more
809 heavily attacked ones of *T. korupensis*. Furthermore, and separately, at the end of January
810 2014 a morphologically different and larger species of caterpillar, yellow-green and behaving
811 very differently from the smaller black one, was seen on five of the 65 monitored *M.*
812 *bisulcata* trees (Appendix 6). Most probably it was another *Achaea* species. Intriguingly, this
813 caterpillar species was feeding on *M. bisulcata* flowers, not young foliage. How influential
814 the new insect herbivore was for *M. bisulcata* phenology that year is uncertain because its
815 distribution was localized to a 2-3 ha patch where the *M. bisulcata* basal area was high.

816 *Tree phenology and masting intensity*

817 Tree phenology of *M. bisulcata* was compared between the heavy mast fruiting year
818 of 2010, and the year of 2012 in which fruiting was very low (Fig. 4; Appendix 2: Table S1).
819 Both time series covered the drought-defined dry season of that year, and followed changes
820 in leaf-flush and leaf-fall (leaf exchange), and flowering, pod formation (green) and pod
821 maturity (brown). Attaining continuous fortnightly scoring was not always feasible and each
822 series has two gaps. Leaf flush likely began a little before the start of the time series recorded
823 for 2010, i.e. earlier than December 2009 (Fig. 4a), but was adequately captured for 2012
824 (Fig. 4b). The bulk of the leaf-flush happened within each year's dry season, flowering well
825 within it in 2010 but coming at the end in 2012. Even though the sum of the flowering scores

826 was similar in both years, fertilization resulted in substantially more green and brown bods in
827 2010 than 2012 (Fig. 4a, b). Caterpillars were not seen in the other years between 2009 and
828 2013, notably not in 2010. In 2010, green pods were apparent between 18 January and 3 July,
829 that is for 5.5 months, with a 1-month overlap as they turned brown between 5 June and 28
830 August, over 2.5 months (Fig. 4a). A similar time course was recorded in 2004 (Newbery et
831 al. 2006a), and likewise (for green plus brown) in 1995 and 2000 (ibid. Fig. 4b). Interestingly
832 the overall period of pod formation was much shorter in the two back-back years of masting
833 1997 and 1998.

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

The presence of the black caterpillar in 2012 appears to have upset the smooth stage-replacement pattern 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 was associated with average green-pod score of 1.7 in May 2013 (n = 33 trees; Appendix 2), showing that masting was more intense there than in the P-plot that year.

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

It is instructive, once again, to look at the course of rainfall events and *rft* during and immediately after the dry seasons of 2009-2010 and 2011-2012 to find clues for the second, early March, caterpillar attack. This last came during a second short dry period when there was that unusual third leaf flush (Appendix 6: Fig. S2c; cf. Fig. 4b). With an interval of ca. 14 days between phenology census recordings, it is difficult to say which came first; but the most likely explanation is the further dry period caused flushing and this promoted renewed

876 feeding, possibly from a next cohort of caterpillars that year. The dry season 2009-2010 had
877 also several dry days at a similar time but broken by a large wetting event (and there was no
878 further flush after the dry season one). For comparison, the pattern of 2010-2012 shows the
879 shorter, late-starting and not so intense, dry season for a typical non-masting year (Appendix
880 6: Fig. S2b).

881 *Palm-oil yield comparison*

882 An analysis of the monthly yields of palm oil, for 2003 to 2016, from plantations
883 adjoining KNP (Appendix 7), showed no year-to-year differences in means attributable to
884 changes in either rainfall or radiation, although there was a very clear repeating pattern for
885 each of the three variables within each year. Moreover, mast fruiting of *M. bisulcata* in this
886 period (see Fig. 1a again) did not correspond to peaks or lows in this proxy measure of
887 productivity, for either the current or prior year. The poor relationship with radiation also
888 means that yield cannot *inter alia* be used in an inverse estimation to confirm the interpolated
889 missing months of radiation at Bulu in 2009-2011 (see Appendix 1).

890 *Stem increment growth from coring*

891 Annual radial increments (*incr*, mm) in stem growth of 20 cored *M. bisulcata* trees ≥
892 50 cm diameter in the P-plot (see Newbery et al. 2013) were matched to occurrences of
893 masting over the 15 years of 1989-2003 (Appendix 8: Fig. S1a). The end date was the last
894 reliable year which had a reliably-determined annual band for all trees. Standard deviation
895 increased linearly with the mean over years (slope [CV] = 1.14, adj. R^2 = 50%, P = 0.002),
896 indicating a considerable variability in increment between trees in any one year (Appendix 8:
897 Fig. S1b). No masting was noted for 1988 (Newbery et al. 1997) but that is not fully certain.

898 Linear mixed-effects models were run using ln(*incr*) as the response variable, trees as
899 subjects (or 'blocks') and ± 'M' as the factor. A binomial logistic regression fit of masting

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

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

Binomial logistic regression fits of masting for 1989-2003 to mean annual core increment with either *radi* or $radi_{sr}$ (current or prior year for both variables) were all insignificant for the increment term (current: $P = 0.49$ to 0.63; prior: $P = 0.46$ to 0.95). The same approach applied using increment of the year prior brought little improvement in fitting ($P = 0.18$ to 0.33; $P = 0.18$ to 0.62, respectively). Thus whilst increment and dry-season

925 radiation remained significantly positively correlated (r = 0.532, df = 13, P = 0.041),
926 partialling out radiation effect was of little avail in unravelling a fruiting-stem growth
927 interaction.

928 *Nutrients in the masting interval*

929 The newly-reported nutrient data, coming from the approaches described in the
930 'Methods' section above, are combined here with other nutrient data already published. To
931 begin with, for 1997 and 1998, and for 2011, the leaflet-to-rachis ratio of N was 1.568 and
932 1.524, and correspondingly for P it was 1.344 and 1.274 respectively, with means of 1.546
933 and 1.309. For 2011 only the L/R ratios for K and Mg were 0.540 and 1.686. It was striking
934 how much higher was the K concentration in the rachises compared to leaflets.

935 In the 1990-1992 litter sampling the bulked samples each represented 0.320 ha of
936 forest. In 2011 sampling the trap clusters represented on average 0.368 ha. This means that
937 each nutrient value is similarly based on ~ 1/3 of a hectare, and the respective samples sizes
938 of 5-and-5 versus 30 can be retained in statistical comparisons without needing to group the
939 2011 ones. Likewise, the 1997-98 study used some of the same half-plots, and accordingly
940 had the same scale as in 1990-92. Working with the typical masting cycle of 3 years shown
941 by *M. bisulcata* at Korup over the period 1989-2010 (Newbery et al. 1998, 2006a), the three
942 sampling dates together allow a series of immediately-after (2010-11), and 1 (1990-91) and 2
943 (1991-92) years after (and thus also immediately before the next), masting events to be
944 constructed. The two consecutive years are likely temporally correlated, but the time
945 difference between them and 2011 is large. The further data from 1997-98 present an
946 interesting comparison in that masting in 1997 had evidently not prevented a repeat even the
947 following year. Over the successive four fortnights, concentrations of N were 18.69, 17.20,
948 18.58 and 18.63 mg g^{-1}, and those of P were 0.802, 0.799, 0.787, 0.956 mg g^{-1}.

949 The concentrations across the three weekly litter samples in December 2002 (Schwan
950 2003), were averaged per trap. To obtain whole-leaf concentrations, the averaged values per
951 tree were first divided by the 1997-98/2011 leaflet-to-rachis ratios to have indirect rachis
952 estimates, and then the 4:1 leaflet-to-rachis mass ratio was applied. This assumed that the
953 ratios from the 1997-98 and 2011 studies could be used here for 2002 (which lay between
954 them). For the complete five-element data sets and direct estimation of leaf concentrations in
955 Table 2 (viz. 1991-92 and 2011), years 1-3 after masting, N, P, K and Mg all differed
956 strongly and significantly (F = 13.4, 12.2, 27.2 and 6.01, all $P < 0.01$) but not Ca (F = 1.0, P
957 > 0.05).

958 The results show that in the inter-mast period, N was low for the first two dry seasons
959 and then rose the year before the next masting, P increased from low to high approximately
960 linearly in the period, Ca barely changed, K and Mg were relatively high for the first two
961 seasons but fell in the third before masting (Table 2). This suggest that N and especially P
962 concentrations were depleted by the last mast fruiting and were re-instated before the next
963 event. K and Mg increased earlier in the interval but were presumably deployed elsewhere
964 before masting. Despite the different sampling approaches, standard errors of means, across
965 years per element, were quite similar. The concentration within the double-masting period
966 1997-98 intriguingly lay between the 1991 and 1992 ones for N, but were higher than both of
967 them for P. That P was accumulating before masting is clearly demonstrated. The rise in P at
968 the end of the litter fall series, but not of N, in 1998 is also remarkable (Table 2). The 1998
969 litter was collected immediately before a masting like the 1992 one, so they could be
970 considered comparable in this respect even though the previous mast fruiting events were 1
971 (unusually) and 3 years prior respectively. Averaging the 2011 and 2002, and separately the
972 1992 and 1998, values where possible in Table 2 gives composite estimates of leaf
973 concentration respectively immediately post and prior to masting: N: 16.73, 18.80 (+12.4%),

974 P: 0.615, 0.825 (+33.9%), K: 5.00, 2.44 (–51.1%), and Mg: 3.42, 2.53 (–26.0%). These inter-
975 mast changes suggest that N and P were depleted by fruiting and restored for the next event—
976 proportionally three-fold more for P than N, but the opposite occurred for K and Mg.

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

984 *Microberlinia bisulcata* leaf litterfall rates in the 12-month July-to-June periods of
985 1990-91 (non-masting in 1991) and 1991-92 (masting in 1992)—found by integrating the
986 areas under curves of litter fall versus time in Chuyong et al. (2000: Fig. 2d)—were
987 practically the same (1710 and 1670 kg ha^{-1} yr^{-1}, respectively). Multiplying these values by
988 their corresponding P concentrations (Table 2), led to a difference of 0.168 kg P ha^{-1} yr^{-1},
989 which is very close to 50% of the investment in masting in 1998 (Table 3), assuming that the
990 mast fruiting that year was similar in intensity to the one in 1992.

991

992 DISCUSSION

993 *Mast fruiting – a non-stationary process*

994 If masting is driven by availability of resources, and these are partly stochastic and
995 partly trending over time, then a range of interval lengths might be accommodated for *M.*
996 *bisulcata*. In reality this range is limited to 1 to 3 years. The extended time series showed that
997 between 1989 and 1995 there was a 3-year cycle, but after 1995, as radiation increased, there

998 came a double year 1997-98 with high fruiting—1998 somewhat weaker than 1997, and then
999 the cycle dropped to 2 years with a masting sequence 2000, 2002, and 2004, returning to very
1000 strong masting in 2007 and 2010 on a 3-year cycle, and finally after that the control
1001 seemingly weakened and resulted in two double-years, 2013-14 and 2016-17, which showed
1002 only moderate mast fruiting. Apart from being quite short at 29 years, the time series was
1003 non-stationary. There would be little reason to assume that it would a priori be stationary,
1004 especially, given the late transient cycle stage of the stand (Newbery et al. 2013) and the
1005 varying climatic variables on all time scales ranging from years to decades and centuries
1006 (Nicholson et al. 2000, 2018). The inconstancy might be best understood in a novel way with
1007 a two- or three-factor threshold model, where C, P and K reach potentially different
1008 thresholds, simultaneously or sequentially. Thresholds themselves may not even be constant
1009 over time but relate to age, climate trends, and other tree-internal demands. When one of the
1010 resources reaches its threshold early, its effectiveness could be limited by the slower
1011 accumulation of another resource. The first resource will need to be stored or allocated
1012 elsewhere in the tree, even to then support the faster acquisition of the lagging resource. In
1013 time the second resource accumulates to a level that crosses a pre-set threshold, and this then
1014 allows the first resource to come into operation.

1015 The allocations of C to mast fruiting in *M. bisulcata* are substantial. The earlier mast
1016 fruiting event of 1995, 28 out of 30 trees recorded had fruits. The average number of seeds
1017 per tree was ~26K (maximum 92K). Using estimates of mean dry masses of seeds and pods,
1018 and mean numbers of seeds per pod, the total dry mass investment was 17 and 307 kg per tree
1019 respectively, summing to 324 kg per tree (Green and Newbery 2002). These per-tree masses
1020 translate to 53 plus 981 = 1034 kg/ha, ~55% the mass of average annual leaf-fall (Green and
1021 Newbery 2002). Applying the individual seed and pod masses to counts made for the 2007
1022 and 2010 events, for trees that had pods (Norghauer and Newbery 2015), gave 181 kg per tree

1023 in 2007 and 122 kg per tree in 2010. (Excluding the two zero-producers, output values for
1024 1995 were 346 kg/tree.) On this basis the investments per masting tree in 2007 and 2010 were
1025 52 and 35% respectively of that in 1995, illustrating an up to almost two-fold variation in
1026 masting intensity across these full fruiting events. Other more semi-quantitative scorings of
1027 mastings across the rest of the time series suggest a similar range in reproductive output.

1028 Flowering is a precondition to fruiting, but the dependence is not exact. Heavy
1029 flowering was recorded in 1992, a mast year; but in 1991 there was also especially heavy
1030 flowering but no mast fruiting (Chuyong 1994, Newbery et al. 1998). In 1990 there was some
1031 low fruiting (flowering unmonitored), this coming though in the year after a main mast
1032 fruiting in 1989: further, 1993 had very little flowering and consequently almost no fruiting,
1033 and 1994 relatively high flowering but only scattered individuals fruiting Green and Newbery
1034 2001a, 2002). From the later, more detailed, phenology recordings, 1995, 1997, 1998 and
1035 2000 had strong flowering and were masting years, whilst 1996 and 1999 flowering was
1036 practically absent and had no masting (Newbery et al 2006a). Whilst valvate bracteoles
1037 protect flower buds before anthesis, it is possible that the intense occasional shower could
1038 damage flowers enough to interfere with pollination. This is the surmise for 1991, two years
1039 after the 1989 masting: fruiting was probably checked and masting was delayed to 1992. In
1040 2004, the dry season started 43 days after 1 December 2003, on 12 January 2004 (Newbery et
1041 al. 2006a): recall that the dry season for a given year starts in December the year prior.
1042 Flowering peaked over the week before and after that date. But in 2012, the season started 21
1043 days in, on 22 December 2011, which was 1 month before flowering started in 2012, and
1044 ended another month later. (In both 2004 and 2012 there were no heavy showers that could
1045 have disturbed pollination in the first halves of those dry seasons.) These facets indicate that,
1046 firstly, occasional external and unpredictable influences can alter the processes behind a
1047 masting cycle; and secondly, the timing of flowering (also linked to the timing of leaf-

1048 exchange) can change by up to a month with respect to the start of the dry season. If internal
1049 tree nutrient levels do, via deterministic physiological mechanisms, trigger the flowering—
1050 which leads most often to fruiting at some level of strength (Newbery et al. 2006a), masting
1051 remains also subject to any climatic stochasticity causing interference to pollination (may be
1052 once in 10-15 years) and variability in dry season timing and intensity (every year).

1053 Abortion of small immature green pods falling to the ground was not seen in the 29-
1054 year period. It remains possible that outside of the three more intensively recorded periods
1055 this phenomenon was missed. If in occasional years there was strong flowering but no mast
1056 fruiting followed, then usually those trees that did develop any pods carried them through to
1057 maturity. The control of masting therefore most likely happens before flowering (see
1058 Newbery et al. 2006a for further discussion). After that seed failure is simply a chance
1059 unpredictable cost within the evolved life history schedule.

1060 *Nutrient resources — interdependencies*

1061 Analysis of the seed and pod nutrient concentrations and amounts in relation to those
1062 in mature leaves indicated ratios of between ~ 0.1 and 0.2 for N, P, Mg and Ca, but
1063 substantially higher at 0.6 for K. This difference is very largely due to the low concentrations
1064 of the first four elements, and a much higher one for K in the pods. Pods were collected
1065 recently fallen. Caesalp pods are hard and rather water-repellent for several weeks, so it is
1066 very unlikely they adsorbed much K coming down in canopy throughfall (G. Neba, D. M.
1067 Newbery and G. B. Chuyong, in prep.), or were they leached to any extent. Had that been a
1068 cause of an increase, then Mg should have increased too, yet it did not. Presently it is difficult
1069 though to explain why so much K was being invested in pods. The comparative leaf K values,
1070 coming admittedly from a retranslocation study where replication of bulked samples per date
1071 was small, do closely match those of mature leaves of plantation-grown *M. bisulcata* trees

1072 (averaging ~ 5.8 mg $g^{-1;}$ at ages of 13 to 18 years; D. M. Newbery unpubl. data). Whilst
1073 ECMs are strongly linked to P acquisition and uptake in the P-poor soils, K is also very low
1074 in availability at Korup (Gartlan et al. 1986), and the surface-soil root mat (with dense
1075 mycorrhizal networks) is an efficient collector of K (and Mg) coming down in throughfall (G.
1076 A. Neba, D. M. Newbery and G. B. Chuyong, unpubl. data). In plots at the same site,
1077 Chuyong (1994) found N, P, K, Mg and Ca concentrations of 13.8, 2.09, 6.41, 2.22 and 3.50
1078 mg g^{-1} respectively in *M. bisulcata* seeds that fell in 1992. Pods were not separated in the
1079 1992 general collections but included within 'all reproductive parts' in the HEM plots, those
1080 with high abundance of *M. bisulcata* had a mean K concentration of 6.04 mg g^{-1}. Although
1081 other elements in fruits were albeit a little higher than for *M. bisulcata* alone in 1998, the
1082 earlier data well confirm the K values of interest. Investing P in seeds would presumably be
1083 important to the survival of establishing seedlings up until they could become infected with
1084 ECMs and link into the mycelial network. Could it be that also K, not P alone—as for some
1085 time thought (Newbery et al. 1988, 2002), is a second key controlling element of masting in
1086 the Korup groves, or as several indications suggest P and K might act synergistically?

1087 The main pattern explaining the masting time series was the sequence of relatively
1088 wet dry season followed by relatively dry one. There was no evidence of water limitation to
1089 large trees in the dry seasons because of their ability to root deeply (Newbery et al. 1997,
1090 2009), so this points to a soil or nutrient factor governed by soil moisture content, in the
1091 upper soil layer where fine roots and ECMs, form a root-mat, are most abundant and active in
1092 nutrient cycling. What is it about relative dryness and wetness of the dry months that leads to
1093 these relationships? Possibly dryness affected the fine roots and ECMs. The drier the dry
1094 season, then likely the more restricted the root activity under limiting surface soil water
1095 conditions; which would possibly signal stored P in the ECMs to be moved to intermediate
1096 locations ready for fruiting, and less would be used in maintaining new root growth. In a

relatively wetter dry season this root activity would continue longer and more effectively, so that any additional P stored in the roots would stay there and not be signaled away to fruiting. Nevertheless, the main mineralization and uptake occurs in early weeks of the wet season (Chuyong et al. 2002), and this would be similar each year once the water contents were high enough. This dryness then 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 1997-98.

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 which leaves 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).

1122 A cycle of 3 years would most likely allow a restocking of P, not only enabling
1123 growth of other tree parts, but also storage of P in wood rays and roots ready for fruiting (as
1124 the model later explains). A 4-year cycle could arise but, *ex hypothesis*, that would need a
1125 sequence of two dry dry-seasons: none was recorded however. The regression modelling
1126 gave an indication that year-to-year increases in radiation, and positive deviations from the
1127 smoothed trend of radiation with time. Changes were relatively small, radiation varied rather
1128 little from year to year, both for the dry seasons and the years as a whole. The additional
1129 radiation probably did not contribute to much increase in photosynthesis which would cater
1130 completely for the extra demand in years of masting, above the potential competition for C by
1131 leaves, stems and roots. Variation also in start and duration of the dry season, with the fairly
1132 steady daily radiation inputs, meant that there was probably sufficient radiation supplying C
1133 on top of tree storage, to meet the high dry mass investment in fruits. Carbon supply was
1134 therefore likely not the limiting factor to masting. One way to resolve this possible
1135 contradiction is to propose that, internal to the tree, there was strong temporal division in the
1136 allocation of C between rooting (one year, more wet) and fruiting (the next, more dry).
1137 Further, the lack of a relationship between proportion of crown fruiting and tree size may be
1138 further evidence that C is not the primary limiting factor for mast fruiting (as was originally
1139 suggested by Green and Newbery 2002), if it can be assumed that large trees store more
1140 NSCs than small ones. The lack of year-to-year differences in oil palm yield relating to
1141 radiation is also moderate evidence of C from photosynthesis not being so critical for their
1142 yielding either. Palms can store up to ~20% of their C in stems from year to year (Corley &
1143 Tinker 2016, Legros et al. 2009). The lack of correspondence between oil palm yield and *M.*
1144 *bisulcata* fruiting suggests no common climatic driver and points indirectly to nutrients as the
1145 key factor in the forest, though possibly not P alone since palms did not respond to P
1146 fertilizer.

1147 The very few studies on C and nutrients involved in mast fruiting of dipterocarps that
1148 have been made largely support the thesis of this paper. Defoliation and girdling experiments
1149 on branches of *Dryobalanops aromatica* trees by Ichie et al. (2005b) indicated that flowering
1150 drew on C stored in local branches and the filling of fruits came from nearby leaves. This
1151 confirms the many similar conclusions for temperate trees mentioned in the *Introduction*.
1152 Relative allocation of P to fruits was shown to be higher than of C and N for of another
1153 masting dipterocarp, *Dipterocarpus tempehes* (Ichie et al. 2005a), again emphasizing the
1154 importance of P in reproduction, especially on P-poor tropical sites. During a different
1155 masting event for *D. aromatica*, Ichie and Nakagawa (2013) found that P concentrations in
1156 branch, stem and roots steadily decreased during flowering and fruiting (but not in twigs and
1157 leaves), N fluctuated slightly (in all parts) and, whilst K decreased during flowering, it
1158 increased during fruiting (in all parts). Of the P needed for fruiting, 68% was estimated to
1159 come from branch storage, compared with only 20% for N and very little for K. This was the
1160 first time root-stem-branch stored P was shown to be important for masting, and the result
1161 corroborated the hypotheses of Henkel et al. (2005) and Newbery et al. (2006a). A further
1162 study at the forest stand level provided more support for P and K both being key nutrients in
1163 mast fruiting. Aoyagi et al. (2018) followed nutrient fluxes in soil, stems and fine litter in a
1164 lowland dipterocarp forest during one such event and for 4 years afterwards. Fluxes of P and
1165 K were much higher in total fine litter in the mast year than later years, whilst those of N, Ca
1166 and Mg altered little; the higher P and K was coming from the high allocations to fruits.
1167 Interestingly, P and K concentrations in coarse roots—but not stems—of the most abundant
1168 dipterocarp, *Shorea multiflora*, decreased more in flowering than non-flowering trees. This
1169 might indicate root storage of P and K ahead of stem and branch storage, in preparation for
1170 fruiting. Kitayama et al. (2015) have more generally demonstrated in NE Borneo that across a

1171 P-use efficiency gradient, forest trees allocate proportionally much more P than C or N to
1172 reproduction (in relation to total allocation), even at P-poor sites.

1173 *Related considerations concerning carbon*

1174 The internal distribution of C between potentially competing sinks within each tree
1175 has a further interesting aspect. A majority of the *M. bisulcata* trees in the grove are presently
1176 of large to very large (≥ 50 cm stem diameter) sizes which means they likely have
1177 considerable respiration and maintenance costs. C at least would not be so readily available in
1178 an average year to sustain such a heavy fruiting without causing deficits in growth elsewhere
1179 in the tree, perhaps in fine roots and ECM production. This would lead, hypothetically, to an
1180 even stronger competition between rooting and fruiting, once stem growth is partitioned
1181 aside. That seedlings and saplings survive very poorly close to adults, led to the proposal of a
1182 reverse drain operating towards the old adults especially in mast fruiting years, for P as well
1183 as for C (Newbery et al. 1998, 2006b, 2010; Norghauer and Newbery 2016).

1184 Previous estimates of leaf litterfall were 1880 and 1380 kg ha^{-1} yr^{-1} in non-masting
1185 1990 and masting 1989 respectively (the first estimate is used in Table 3), and came from
1186 Green and Newbery (2002), who in turn based their calculations on January-to-December,
1187 plot-level, leaf litterfall estimates given in Newbery et al. (1997). The 1990-92 data later
1188 indicated 39% of that litter was from *M. bisulcata* trees. This 0.74:1 ratio may have been an
1189 overestimate, because it used calendar year estimates which would have missed linking
1190 November-December litterfall with that in January to April prior to masting, and the newer
1191 1990-91 species-specific data were more precise. Or, it simply reflects variation in litterfall,
1192 viz. 1380, 1880, 1710 and 1670 kg/ha over the four years 1989 through 1992, which suggests
1193 that C supply was likely again not to have played an important role in determining mast
1194 fruiting since in around one masting event there was an implied cost to leafing and around the

1195 other none. The fruit-to-leaf amount ratios and reproductive allocations percentages in Table
1196 3 may well be ~10% lower than the true values, if the 1990-92 litterfall estimates did apply.
1197 The 1990-1992 data also display a small shoulder in May 1992, possibly the result of the last
1198 older leaves being exchanged for the new green pods.

1199 Green pods stay on the trees for more than 5 months and therefore will contribute C to
1200 their structures and to developing seeds. This is likely an important source, and pods and
1201 seeds may indeed be almost autonomous in this respect. Pods are also held up high on the
1202 outer canopy edges where their photosynthesis is maximized (Norghauer and Newbery 2015).
1203 Bennett et al. (2011) reviewed the role of pods in their photosynthetic capacity, and Zhang et
1204 al. (2016) provide a detail analysis of C balance in pods of *Medicago sativa* showing the
1205 considerable C inputs that are possible. This source of C would make the *M. bisulcata* trees at
1206 masting even more independent of C stores within the rest of the tree. It might explain the
1207 effect of raised radiation in the current fruiting year when compared with the one prior.

1208 That stem increment growth was positively related to current year radiation but mast
1209 fruiting was not always, or at least not so strongly, suggests that C from photosynthesis was
1210 being used for stem growth and in mast years it was additionally contributing to mast fruiting.
1211 An internal trade-off between root growth plus ECM activity to enable the uptake of nutrients
1212 allowing nutrient uptake, and an allocation to fruits and seeds when cued may probably well
1213 be the basis to the masting cycle. In the year following a masting relatively more C would be
1214 allocated to roots because, if fruiting is 'switched off', roots become the main alternative
1215 sink; and then if in the second year there is sufficient P to cross the threshold, with an
1216 increase in radiation and extra C input, a next masting would occur after 2 years. If P
1217 accumulation was limited the tree would wait until the next year, a 3-year cycle. Extra C
1218 available in that second interval year might then determine the intensity of the masting ('M'
1219 or 'm'). A notable difference between P and K, is the rate of change in concentration in the

1220 leaf litter as the interval between mast fruitings progresses: P increased slowly over 3 years
1221 but K rose rapidly then fell lower than at the start. This might imply faster recycling of K
1222 than P, with a stronger withdrawal of K than P at senescence later as storage cells were being
1223 refilled prior to masting.

1224 *Rainfall and nutrient uptake*

1225 The important effect of mean daily rainfall in the dry season is dependent on the
1226 pattern of rainfall distribution over time, through the dry season and just into the early wet
1227 season weeks, that is up until the 100 mm threshold defining the season is exceeded. The first
1228 week's rainfall governs root growth and ECM physiology, and the later ones connect to the
1229 early wet season and the throughfall which primes the start period of optimal leaf litter
1230 decomposition (Chuyong et al. 2002, 2004). A dry season may well limit root activity, and it
1231 also would delay decomposition: one which was short would only affect the former. On the
1232 other hand, a relative wet dry season will be expected to restrict rooting and ECM activity
1233 much less and encourage the earlier start of decomposition, both processes leading to better
1234 nutrient uptake into the trees. ECM activity doubtless plays a role in P uptake, and the
1235 regrowth and maintenance of the root mat itself determines the level of retention of K leached
1236 from the canopy and its uptake.

1237 An important aspect in connection with P-supply for fruiting, is how P is taken up and
1238 stored in inter-mast years. In the dry season of 1988-89 and 1990-91 there were pronounced
1239 peaks of P in fallen leaf litter in the HEM but not LEM plots (Newbery et al. 1997). This
1240 peak was absent in 1989-90, directly after the heavy mast fruiting. The HEM litter would
1241 have been composed of ~80% *M. bisulcata* leaves (Chuyong et al. 2000). In a relatively dry
1242 dry-season with likely more fine root and ECM die back than in a wetter one, P might be
1243 translocated out of these fine roots and ECMs, going into storage for fruiting. Taken together

1244 the integrated aspects of this P nutrient cycle do provide reasonably strong support for P
1245 storage and use leading up to, and during, the masting events.

1246 Another result providing important evidence for P-storage is from the comparison
1247 between concentrations and amounts in the years across masting intervals which suggests
1248 further that the 50% of P used in masting was coming from retranslocation of P out of
1249 senescing leaves a few months before, probably stored in branches; and by difference it might
1250 be deduced that the other 50% was older and coming from local branch/wood storage built up
1251 in the prior 1 or 2 years, still within the interval. That result would fit with the notion of a
1252 temporary store for P and not all of the P needed for masting could be supplied in the current
1253 year alone. Rosell et al. (2020) in a study of a range of tropical tree species found the inner
1254 bark of branches was especially important for NSC storage and, although not yet tested, this
1255 may be where P is also held, ready for fruiting. Jones et al. (2019) indicate this as a
1256 possibility for premontane tropical forests.

1257 If P in leaf litter is relatively low in concentration after allocation to fruiting (Newbery
1258 et al. 1997, and new evidence in this paper), then the fast-forward cycling proposed by
1259 Chuyong et al. (2000) could be temporarily slowed because mineralization by saprophytic
1260 fungi would have a low P litter resource to decompose. Root activity would either need to
1261 become more intense and efficient to take up the now lower soil levels, or at this time the
1262 ECM activity would come more to the fore by not only accessing low molecular-weight
1263 organic P molecules efficiently but also by effectively reaching low-concentration inorganic
1264 P sources further way from roots. This impasse would strongly select for the several co-
1265 adapted root mat and ECM traits seen in the field in order to achieve restocking of P. The rise
1266 in P accumulated just before masting could lead to higher P in litter falling that year which on
1267 one hand would mean fast re-uptake but on the other appears to be a dissipative risk when the
1268 perceived strategy is to save P (in the tree) for immediate use in fruiting. However, the ECMs

1269 being part of the whole tree system, and cycling highly efficient, P is being 'saved
1270 dynamically' within the nutrient cycle. Also, N and K would in parallel complement C in
1271 stores — the latter benefitting from the small increase due to radiation enhanced
1272 photosynthesis, all three also needed for seeds and pods. That P was high in falling litter just
1273 prior to masting might furthermore indicate that P stores were quite full after a 2-year
1274 interval, and some of that 'extra' P was also coming from root retranslocation.

1275 The analysis of mast fruiting in 1989-2004 (Newbery et al. 2006a) used 150 trees
1276 across the whole P-plot, but the later recording 2009-2014 used a subset of 61 trees in the
1277 eastern half, an area 100-500 N by 1000-1200 E, on the higher ground with denser stands and
1278 larger trees. The masting time series could potentially have been confounded then by
1279 sampling extent changing over time, because for the earlier half (1989-2004) it was found
1280 that masting was significantly stronger on the relatively higher and drier sites of this eastern
1281 part of the P-plot compared with the rest of the plot (Newbery et al. 2006a). Allaying these
1282 doubts, the full and strong mastings in the second half (2007 and 2010) were confirmed by
1283 seed trapping across the entire plot (Norghauer and Newbery 2015). The two double-years, in
1284 the second half of the time series, were only moderate mastings despite being at the more
1285 favorable topographic location.

1286 The very strong mastings achieved by *Dicymbe corymbosa* in Guyana are associated
1287 with pronounced ENSO peaks in radiation (Henkel et al. 2005, Henkel and Mayor 2019).
1288 However, this ectomycorrhizal caesalp, although phylogenetically very close to *M. bisulcata*,
1289 is unusual in that it reproduces annually also by sprouting, which must impose a considerable
1290 demand on C and nutrients for growth. For this reason, it might be conjectured that C stores
1291 are probably being continually used up and hence, to achieve a mast fruiting, a dependence
1292 on an additional boost in incoming radiation in those ENSO years would be necessary. Again,
1293 in contrast to most of African caesalps (including *M. bisulcata*), one other caesalp

Gilbertiodendron dewevrei—which forms monodominant stands in Central Africa—also exhibits mast fruiting (quite unsynchronized spatially, and at irregular intervals) but its seeds are very much larger (~ 30 g; Hart 1995) so the mass allocated to reproduction is far more than for *M. bisulcata*. Compared with SE Asia and C. and northern S. America, the lack of a strong ENSO signal in C. Africa is pertinent (Camberlin et al. 2001, Poccard et al. 2000). Masting in dipterocarps may well be for different suite of factors from those controlling the caesalps, achieving an evolutionary stable strategy along an alternative channel.

The interference effect of herbivores

The loss of a 2- or 3-year cycle in masting after 2011 suggests that the rhythm of wet/dry dry-season release of nutrients needed for full masting was disrupted by a combination of lack of an alternating pattern in rainfall plus heavy caterpillar attacks. This latter unforeseen intervention, combined with a chance climate regularity over 3 years, acted as a 'quasi-treatment' in that C gain and storage were likely temporarily reduced. From the above argumentation it was not so much the decrease in C to supporting fruiting that was alone important but also the loss of C input for roots to allow P to be taken up and accumulated even in the relatively wet dry seasons. With some commitment to flowering already, leaf grazing would have nullified any C input from the local branches attacked to fruiting, requiring the tree to draw on stores in the branches. Nevertheless, some fruits resulted, indicating a means by which tolerance to herbivory could have occurred (Norghauer et al., 2023). The caterpillar attacks may have interfered with the accumulation of P and thereby interrupted masting in full, leading to the unusual double 'm' years. The evidence of an herbivore effect is strongest for fruiting in 2013-14 because of the detailed phenology data in 2011-12. It is tempting to suggest that something similar might have been happening in 2015 before the very similar masting pattern of 2016-17: alas, herbivore and tree phenology records were not possible during those later 3 years. A further unknown aspect is how

1319 herbivory may have induced stress hormones in the trees which, interacting perhaps with K
1320 levels, affected cytokinin concentrations.

1321 The pooled field notes and observations suggest two lepidopteran herbivores occur in
1322 the crowns of co-dominant *M. bisulcata* and *T. korupensis* in the natural old-growth forest of
1323 Korup. Both species have pinnate leaves—*T. bifoliolata* does not—and similar stem density
1324 (~ 3.5 per ha for ≥ 50 cm DBH; Newbery et al. 1998), but *M. bisulcata* trees are the greatest
1325 in size with a near-zero mortality rate (Newbery et al. 2013). If caterpillars indeed fed only on
1326 expanding leaves (or flowers), then severe damage could ensue quickly, within 1 to 2 weeks,
1327 inducing premature abscission (or lost pollination). For example, within 1 week caterpillars
1328 defoliated young leaves in crowns of two monodominant leguminous tree species in rain
1329 forests of Brazil and Gabon (Nascimento & Proctor 1994, Maisels 2004). Such phenomena
1330 are quite easy to miss though. This could explain why the black caterpillar was not noticed
1331 before at Korup, but it is unlikely the reason for the yellow-caterpillar given the extensive
1332 phenological monitoring of *M. bisulcata* (Newbery et al. 1998, 2006a; Norghauer et al.
1333 2023). The detailed monitoring between 2009 and 2013, like that between 1995 and 2000, did
1334 not note any caterpillar attacks. To have an importance they would surely have been seen
1335 before from their feeding effects (droppings, noise of chewing, fallen individuals, hanging
1336 threads, frass in traps). Many other periods of intensive work back to 1984, focused in the dry
1337 months and into the early wet season when caterpillars would occur, did not record them.
1338 Whether these outbreaks are triggered by favourable climate factors, or palatable leaf
1339 chemistry or less parasitoid pressure, either perhaps induced by drier conditions (van Bael et
1340 al. 2004), or simply mounting abundance over years (Wong et al. 1990), is unknown.
1341 Herbivore attacks to flowers, occurring stochastically, might be viewed as being similar in
1342 end effect to intense rainfall events disrupting pollination: both limit reproduction.

1343

1344 *Refined updated hypothesis for mast fruiting in caesalps*

1345 The mast fruiting cycle in *M. bisulcata* might be explained in terms of the availability
1346 of three principal resources which control the timing of reproductive output: the limiting
1347 resource P, a controlling resource water, and qualifying resource C. If sufficient P
1348 accumulates within 2 years to trigger flowering and there is sufficient C coming from storage
1349 laid down over the last year or supplemented due to a positive radiation difference between
1350 prior to current year, then fruiting is to be expected. But when P is slower at accumulating,
1351 the interval is extended by one year and fruiting happens within 3 years. It is highly likely
1352 that in the latter case C would still be sufficient either from reserves laid down in the tree in
1353 the previous year and/or a small surplus the current year of fruiting. When there is sufficient
1354 P accumulated after one year but not quite enough C for a full masting, fruiting may follow
1355 anyway at a moderate level; and in doing so it is likely that not all of the P accumulated
1356 would have been allocated 'as planned', and the part remaining, plus last year's continuing
1357 uptake, will sustain a second moderate fruiting. On grounds of resource requirements, it is
1358 difficult to see how the pattern could be 'm-M' or 'M-m', and neither of these were observed:
1359 in the first, there would be insufficient time after a 'm' fruiting to build up P so rapidly to
1360 have an 'M' one, and in the second, the 'M' first would exhaust P levels down below a
1361 threshold and no 'm' would likely be possible either. The pattern M-M did occur once,
1362 however, at the time of an exceptional rise in radiation levels over a 3-4-year period: it can
1363 only be hypothesized that there was unusually even more surplus C for extra root growth and
1364 P uptake in both the year preceding the first 'M' year and during the second one. The main
1365 processes leading to mast fruiting in *M. bisulcata* are schematically summarised in Fig. 5.

1366 An interesting aspect is the feedback control that might operate by way of C going
1367 either into fine roots and ECMs, which would enhance nutrient uptake, or into wood storage
1368 (stem, branch and large root), which could sustain a next fruiting. The 2- or 3-year cycle is

1369 simply a consequence of the contingent conditions of these trees growing in low P soils aided
1370 by ECMs. Rainfall and radiation are stochastic processes, to some extent inversely related,
1371 which overlies the intrinsic deterministic cycle: the important difference between them is that
1372 rain, acting primarily on the soil, facilitates P release, acquisition and uptake (needed to
1373 accumulate P), and whilst C is needed also for fruiting, it is essential for root production and
1374 ECM maintenance that makes this P uptake possible. That root growth should always
1375 precedes fruiting in a masting year, the first in late-dry into early wet season (March-April),
1376 the latter in late wet season (September-October) decides the sequence unambiguously: C in
1377 the dry season will go to the root sink first and what remains stored, used for stem growth or
1378 reserved for fruiting when it happens. The low P supply is therefore the main determinant: C
1379 must be sufficient but does not appear to be decisive for the interval length. N and K will also
1380 be involved but the evidence more strongly supports the P thesis. Nitrogen is not limiting at
1381 Korup with ample N-fixation and aerial input (Newbery et al. 1997), and whilst K follows P
1382 in being intrinsically quite low in supply in Korup soils, the root-mat appears to be highly
1383 adapted to catching and retaining canopy-leached K and so enabling its efficient recycling (G.
1384 A. Neba, D. M. Newbery and G. B. Chuyong, unpubl. data). The K allocated to pods could
1385 like N be accommodated by wood ray storage.

1386 Carbon and N will be important for masting, even when P and K are limiting and are
1387 the key storage resources, because all elements will be needed in their stoichiometric ratios in
1388 order to fill pods with seeds. As in other plant physiological problems, simplified reductionist
1389 approaches will not recognize the integrated nature of growth and reproduction. Carbon
1390 (sugars) and K are required for transport and storage, P will be bound into C-H-O structures
1391 which act as 'carriers'. It is possible though that a small increase in C from radiation might
1392 have a non-linearly disproportional benefit to P transport and storage. Understanding masting
1393 physiology requires an integrated and dynamic approach, one of shifting sink strengths over

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

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

1419 high flowering per crown then there would be a deficit of C to fill pods, or pod production
1420 would decrease, or another cost incurred (e.g. at the roots or wood production). But the
1421 evidence was that in *M. bisulcata* the relative crown-cover with pods remained constant with
1422 size and, by broad inference, age. As a tree grew to have a larger root system with ECMs to
1423 maintain, to acquire P and retain K, so when absolute pod and seed output rose then the
1424 demand for P and K would also. As with C and N, we can expect that P and K is stored in
1425 'quick-release' forms in wood and back rays of the stem and the main branches. A
1426 phenomenon often remarked is of one part of a large crown flowering and fruiting more than
1427 the others, which could be explained by a correspondingly more active root system of the
1428 tree, and a matching storage of nutrients in the wood and branches, on that side. (See
1429 Newbery et al. 2009 for the strong crown asymmetry in *M. bisulcata*.)

1430 The arguments going from nutrient concentrations in fallen litter through to the
1431 possibly the trees building up and storing P and K before masting are tenuous because of the
1432 many uncertainties about the processes involved. If some translocation occurs out of leaves
1433 before they are shed, then why are the P levels so high just before masting? If P was being
1434 actively stored for fruiting, it might be expected that it would be lower in concentration in the
1435 fallen leaves. However, the high concentration reflects that all the trees were well stocked
1436 with P by that time, the stores were full, or even over-full, and there was still plenty of P to
1437 fall. From earlier work, it was established that ectomycorrhizal species, especially *M.*
1438 *bisulcata*, drop P-richer leaf litter than non-ectomycorrhizal ones (Newbery et al. 1997) partly
1439 because the retranslocation was less (Chuyong et al. 2000), and it was argued then that this
1440 allows the decomposition process to operate without P limitation, the 'fast forward' strategy.
1441 However, the concentration of K (to a lesser extent that of Mg also) reached a peak mid-
1442 interval and then fell just before masting. This could mean that K was being translocated into
1443 storage before fruiting. In general, the export of K and Mg from leaves of trees is usually low

1444 compared with that of N and P. Understanding the differences in dynamics of P and K in this
1445 context is highly challenging, and also explains why N showed no clear mast-interval trends.
1446 Whilst K was likely building up on soil colloids in wetter dry seasons, mineralized from
1447 fallen leaf, dead root and old-pod during decomposition, and this process was more limited in
1448 the drier dry seasons, suggest that K must also have been transported and actively stored in
1449 the tree between the prior and mast years. To recycle more K via litterfall would involve a
1450 potentially high loss due to leaching when the cation exchange capacity of the soil has
1451 already been reached, compared with the seemingly tighter and 'safer' direct access by ECMs
1452 to organic P. This reliability aspect might then favour P over K as the better controlling factor
1453 in masting.

1454 *Phosphorus storage and control*

1455 What could the likely form of storage of P in trees be? Since Bieleski (1973) the most
1456 likely candidate is inositol hexa*kis* phosphate (= phytic acid; $C_6H_{18}O_{24}P_6$). It has been shown
1457 many times to be the main storage form in seeds, and has been detected in stem and roots. It
1458 forms salts with Ca, K, Mg, Mn and Zn, and in soils occurs commonly bound to Fe. It occurs
1459 in 19 hexa-structures which are interconvertible (Raboy 2003). It is viewed as the most
1460 frequent P-storage form when P is in excess, that is in passive storage; the P is readily
1461 retrievable and mobilizable. Other molecules can have seven or eight atoms of P but seem
1462 less common (Raboy 2003). Inositol hexa*kis* phosphate is involved in cell metabolism, in
1463 ATP regeneration, RNA export and the repair of DNA. It is prominent in cell storage
1464 biochemistry, which may make it a candidate for *active* storage. However, so very little has
1465 been researched in this area, and accounts for trees are very sparse. A notable exception is the
1466 study of Kurita et al. (2017), showing P storage in *Populus alba*, followed by release in
1467 spring, and indicating perhaps a common function in many deciduous tree species. It is
1468 conceivable that the same mechanism could operate in seasonal tropical trees and even be a

1469 basis to P storage for mast fruiting species. How inositol hexa*kis* phosphate is linked to
1470 polyphosphate formation in roots and mycorrhizas, and comes under hormonal control
1471 remains unclear.

1472 In an experiment with *Eucalyptus grandis* seedlings, comparing low and high P
1473 media, Mulligan (1988) detected stored P in the form of esters and residual P (mostly
1474 phosphorus proteins), especially in roots, and more so the low P medium. The idea is that
1475 these stores buffer the plant (maybe actively stored), from there P can be mobilized and sent
1476 to other stores in the shoots. In a similar vein, Netzer et al. (2017) comparing mature *Fagus*
1477 *sylvatica* stands, one on high and one on very-low P available soils, found that in the latter P
1478 built up in roots in late summer, and from there was moved on to stem and branches,
1479 suggestive of at least two storage sites in a series enabling adaptation to the poor site.
1480 However, hardly anything is known about how P stores are internally controlled, or how
1481 hormones signal transfers of P (Rennenberg and Herschbach 2013), which could give even a
1482 lead as how P might be built up in stores in masting intervals, and once a threshold level is
1483 met how the switch to flowering is signaled.

1484 Much evidence points to senescence in leaves, and possibly also pod formation,
1485 involving cytokinins too (Marschner 2012). Chiou and Lin (2011) have proposed different
1486 hypothetical models for inorganic P being regulated by cytokinins and sugar levels. How
1487 these promising models can be extended to storage and release of P has yet to be worked out.
1488 The strongest candidate for the elusive 'florigen' is a now widely held to be a flowering locus
1489 T [FT-] protein, which again appears to be controlled by a cytokinin (Turnbull 2011).
1490 Cytokinins act at long distances and are bidirectional in their effects, both of which might
1491 hypothetically implicate them in inositol hexa*kis* phosphate metabolism and P storage. It
1492 remains likely that floral initiation in *M. bisulcata* takes place at the end of the wet season,
1493 before leaf exchange occurs in the dry season (see discussion in Newbery et al. 2006a).

1494 Earlier results on apple (*Malus*) trees suggested already that a two-way process of hormonal
1495 control could be operating (Davis 1957), and the idea that sugars and other NSCs destined for
1496 the usually stronger root sink (Goldschmidt and Golomb 1982, for mandarin (*Citrus*), and
1497 Hansen et al. 1982, for prune (*Prunus*)—on K-deficient soils) might be diverted to the
1498 flowering meristem sinks under the control of gibberellins (Sachs 1977). How exactly the
1499 'switch' occurs remains obstinately elusive (Monselise and Goldschmidt 1982, and to the
1500 present day). The precise consistency of alternate bearing in *Pistacea* orchards has been
1501 questioned on statistical grounds (Rosenstock et al. 2010).

1502 *Active storage hypothesis*

1503 Storage of C as reserves in trees (stem rays, bark and branch wood) was widely seen
1504 in the past as being passive. The C was being made available for regular annual growth
1505 processes in ways that optimized the economy of the tree. (Zimmermann et al. 1971).
1506 Extending this idea to nutrients, Chapin et al. (1990) produced a systematic table for N and P,
1507 reserves of the latter featuring mainly as inorganic phosphate, polyphosphates, or
1508 phospholipids, leading them to conclude that dependence on mineral nutrients is likely much
1509 more pronounced than on C for reproduction. Sala et al. (2012a) argued that the build-up of
1510 NSCs in stores in trees might be acting as a buffer against stochastic variation in C inputs due
1511 to environmental stresses (e.g. drought, herbivore attacks), which as a bet-hedging strategy
1512 would insure against temporary collapses in maintenance and growth. The storage would
1513 need to be active, rather than passive, otherwise in the latter case it would be used up
1514 immediately in extra current growth. Extending this idea to mineral nutrients, Dietze et al.
1515 (2013) hypothesized that N, P and K might also be accumulated and stored to guard against
1516 periods of reduced nutrient uptake, stabilizing the internal nutrient cycles. Hormones might
1517 therefore control source-sink processes actively. The empirical evidence for active vs. passive
1518 control of C storage in trees still remains weak and unresolved though (Hartmann and

1519 Trumbore 2016). But where P and K especially are limiting growth, evolution of such an
1520 active mechanism could be of considerable evolutionary advantage. Mast fruiting imposes a
1521 quasi-unpredictable (partially stochastic) demand on mineral nutrients supplies, and therefore
1522 for P and K active storage would serve it well, particularly in sites where uptake patterns
1523 themselves are subject to environmental stochasticity (the intensity of the dry season at
1524 Korup, for example).

1525 *Nutrients in alternate bearing of tree crops*

1526 Studies of alternate-bearing pistachio trees (*Pistachio vera*) have provided several
1527 valuable insights into how tree nutrient balance changes between 'on' and 'off' years. Whilst
1528 fruiting depresses root growth in fruiting years, uptake rates from the soil remained similar. If
1529 N, P and K moved from uptake mainly to leaves and shoots in 'off' years, and to fruits in 'on'
1530 ones at 3-6-fold the investment compared with 'off'-year uptake, this implies that stores were
1531 being drawn upon (Rosecrance et al. 1996). Trees stored 7- and 14-fold more N and P
1532 respectively in 'off' than 'on' years, mostly in branches, which also suggests active storage
1533 (Rosecrance et al. 1998). Of what went into fruits in an 'on' year, 70% of N and P came from
1534 storage, and 30% from retranslocation. For N and P, storage forms are well known (e.g.
1535 phosphoproteins), but for K they are not. K would need to be intensively taken up in the 'on'
1536 years (study cited here was made on well-fertilized plots, however), despite the slower root
1537 growth, transported and used immediately in the fruits (Brown et al. 1995). Interestingly, K
1538 concentrations in pistachio are inversely related to NSC concentrations, because K is needed
1539 for sugar transport to the apices where fruits are being formed (Marschner 2012). If this last
1540 process applied to *M. bisulcata* at Korup, K would be taken up in the mast years and,
1541 assuming also it cannot be stored in roots or branches, the only other feasible (temporary)
1542 store would be outside the plant, this is as exchangeable forms held on soil colloids, built up

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

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

Soil nutrient status

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

1567 wetter, conditions one year for N supply are not conducive to floral initiation, which depends
1568 more on warm drier ones affording higher sugar transport to apices. An inherent inverse
1569 correlation often exists which leads to an unstable alternation: a similar pattern is proposed
1570 for *M. bisulcata* at Korup with the relatively wetter and drier dry seasons.

1571 Evidence for depletion of nutrients during masting, needing then a restocking for the
1572 next event, is unfortunately limited. For white-bark pines, Sala et al. (2012b) showed that P
1573 and N declined in branches after masting—cones having especially high P concentrations;
1574 and this could be linked to the species being ectomycorrhizal. Depletion spread over other
1575 plant stores according to the amount needed for masting. Not only do Sala et al. (2012b)
1576 provide evidence of resource switching (from storage to reproduction), but weather seems to
1577 be cuing for masting by synchronized nutrient uptake being made possible. This supports
1578 nicely the main thesis of the current paper on *M. bisulcata*. The association with
1579 ectomycorrhizas was not mentioned in the review of Pearse et al. (2016).

1580 Climate factors which affect nutrient resource availability driving masting was a
1581 central argument of the review of Allen et al. (2017). This underlying process is how
1582 economies of scale become operational: the predisposition of trees to avoid seed predation or
1583 increasing their flowering efficacy is enhanced by synchronization. Allen et al. (2017) made
1584 strong recognition of the role of ectomycorrhizas, building on Henkel et al. (2005) and
1585 Newbery et al. (2006). That either N or P (rarely both) are often limiting where
1586 ectomycorrhizas tree species are successfully dominant in forests, must place a high demand
1587 on these elements for seed production. A set of resource acquisition and storage traits that
1588 would benefit growth and defense in these nutrient-poor habitats generally would be expected
1589 to be channel-selected through evolution to support an optimal life history strategy (Allen et
1590 al. 2012). Different storage routes could be postulated to work in temperate vs. tropical
1591 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 rely 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 their availability fluctuates, and tree nutrient concentrations are synchronized via the mycorrhizal network. Stronger competition between masting and non-masting neighbours need not be invoked (as 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.

Janzen (1974) asked why the intervals between mast fruitings 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 (Basnett 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

1642 buttressing, and temporarily supporting suppressed, damaged or dying neighbours, other
1643 advantages of root grafts have not been so obvious (Lohle and Jones 1990). However,
1644 synchronizing nutrient supplies between, and storage within trees, across whole clusters
1645 would clearly be beneficial and strengthen masting. Root grafts would moreover provide a
1646 strong 'platform' for the ECM network and faster local transfers. A role for root grafts
1647 enabling masting has recently been suggested by Noble et al. (2018) to part explain alternate
1648 bearing in pistachio in a year when pollination synchrony (the Moran effect) was relatively
1649 weak. The focus in this plantation study was on C as the putative resource being transferred.

1650 More directly relevant to *M. bisulcata* was the work of Yli-Vakkuri (1953) cited by
1651 Bormann (1966), showing that P was moving across root grafts of *Pinus sylvestris*: the last
1652 author made no connection to ECM status of pines or association of ECMs with mast fruiting
1653 (see Newbery 2005 later). Conceivably, ECM and grafted root-networks might operate
1654 together within *M. bisulcata* tree clusters, either contemporaneously or in successive phases
1655 around the end of the dry into the early wet season. If hormones are also transportable across
1656 grafts, an added level of synchronizing control is afforded. The role of tree root
1657 interconnections (ECMs and grafts) becomes an essential auxiliary to the main masting
1658 hypothesis. Bormann (1966) advanced the thesis that root grafts established first by
1659 alignment of xylem tissues which rerouted water flow and, later, connecting phloem tissues
1660 permitted organic and nutrient transfer. Between the mid- and late-ontogeny stages, *M.*
1661 *bisulcata* trees growing in dense patches become large adults, as described by the transient
1662 dominance model (Newbery et al. 2013), and root grafting may have started when water was
1663 at a premium in the dry season. It then changed to having a more organic-flux transfer role
1664 once deep roots had secured all-year-round water supplies, the root mat had fully formed, the
1665 litter nutrient cycle was stable, and P (and possibly K) were by then in greater demand for
1666 growth and reproduction. To know whether or not codominants *Tetraberlinia bifoliolata* and

1667 *T. korupensis* graft below ground onto *M. bisulcata* would be interesting. That the three
1668 species do not usually mast synchronously suggests, though, that they probably do not form
1669 interspecific connections as predicted by Graham and Bormann (1966).

1670 *Role of environmental stochasticity*

1671 Dynamics simulation models involving storage and thresholds, resource-switching in
1672 a randomly varying environment, yet with no economy of scale operating, are able to
1673 generate masting cycles when either the variation is strong (i.e. very good vs poor years
1674 occur) or, when the variation is not so strong, there is an increasing non-linear response to the
1675 positive variations (Fernandez-Martinez et al. 2017a). Even then masting can be diluted over
1676 successive years and is not quite bimodal. Under weaker variation in the environment an
1677 economy of scale is needed to achieve a well-defined masting cycle (Kerkoff 2004, Lyles et
1678 al. 2009). Such large differences between very good and poor years in terms of resources
1679 (assuming linear responses) are ecologically rather unrealistic though for medium-length time
1680 series covering fairly regular 2- or 3-year masting cycles. This in turn suggests that without
1681 an economy of scale a non-linear response is more likely to be involved. An essential
1682 requirement of such masting would be to avoid degeneration of the time series into chaos—as
1683 shown by the models of Rees et al. (2002).

1684 The systems view would postulate a feedback control to avoid such chaos but it could
1685 allow for an unpredictable mix of 1-, 2- and 3-year cycles over time to the same effect in
1686 thwarting predator tracking. For a limited resource like P, such a system means regulation of
1687 internal fluctuations across the tree parts within a masting cycle, so that some equilibrium in
1688 the P dynamics is maintained medium-term. An economy of scale which itself involves a
1689 mechanism for P distribution would facilitate masting when based on storage and thresholds
1690 of that same resource. In this respect, ectomycorrhizal networks, which enable P acquisition

1691 and uptake (and possibly P storage), could bring about an equilibration of P across the
1692 connected roots of neighbouring trees, which would allow a contemporaneous storing and
1693 triggering of mast fruiting, as P levels rose in concert across all trees in the population (Fig.
1694 5). In the case of *M. bisulcata* in this study, the key climate variables vary in a somewhat
1695 normal way, and it is unlikely they can cue masting in a simple directly-linear manner.
1696 However, if wetter dry seasons lead to non-linear increases, or pulses, of P-and/or K-uptake,
1697 coordinated across the forest, synchrony is also possible. The network idea would also
1698 explain why one or both *Tetraberlinia* species often mast fruit along with *M. bisulcata*,
1699 because they largely share the same mycorrhizal species (Newbery et al. 1988, 2000). The
1700 non-stationary aspect of the main hypothesis suggests a finely-tuned evolved
1701 ecophysiological system in *M. bisulcata* allowing it to respond to variation of the climate in
1702 order to maximize its fitness.

1703

1704 CONCLUSIONS

1705 The results in this paper confirm and extend the findings based on those for 1989-
1706 2004 presented in the Newbery et al. (2006a) with greater statistical detail and confidence. It
1707 would have been valuable to know whether the 3-year cycle returned after 2017. Post-
1708 dispersal predation is currently important, especially in well-lighted gaps although not in the
1709 shaded understorey or below *M. bisulcata* crowns. It could have been much more common in
1710 the past when either *M. bisulcata* individuals were scattered across the landscape (Newbery
1711 and Gartlan 1996), or when transient grove dynamics was at a stage of rebuilding (Newbery
1712 et al. 2013). Since, seeds and seedlings need P to establish and reach to the network of ECM,
1713 it would be evolutionarily advantageous for an ECM species to mast fruit and increase its

1714 chances of establishment. It is interesting that masting is achieved in the most clustered
1715 caesalps, and was not apparent for the more spatially dispersed species in southern Korup.

1716 Most of the C dynamics models for trees to date (e.g. Cannell and Dewar 1994,
1717 Lacointe 2000, Makela et al. 2008, Franklin et al. 2012) do not cater adequately, if at all, for
1718 environmental stochasticity or non-constant reproductive allocation schedules. Source-sink
1719 models for herbaceous plants, let alone for more complicated trees, have made little
1720 conceptual progress in the last three decades since Farrar (1993), Kozlowski (1992), Minchin
1721 and Thorpe (1996), and Wardlaw (1990), apart from raising an unresolved debate over
1722 passive versus active storage. They usually assume steady-state equilibrium conditions, are
1723 often teleonomic (e.g. Thornley and Parsons 2014), and are strongly focussed on stem
1724 diameter growth and maximizing tree yield. They are, therefore, still too far away from an
1725 understanding of trees in natural forest ecosystems (see Le Roux et al. 2001) to explain even
1726 reproductive schedules like masting. Source-sink relationships, within trees especially, turns
1727 out to be very complicated: a more integrated systems approach is probably required. An
1728 important challenge is working out how P, K and N interact with C dynamics over the
1729 complete life-history schedule of a tree. A very interesting hypothesis coming from this
1730 extended phenological analysis is that both K and P levels might synergistically control mast
1731 fruiting of *M. bisulcata*, mediated by the physical structure and functioning of the surface
1732 root mat for nutrient cycling. To test this hypothesis further requires much more detailed
1733 recording of nutrient processes at the tree-level and within the system, replicated over several
1734 mast fruiting events.

1735 The literature review of the likely mechanisms lying behind mast fruiting in *M.*
1736 *bisulcata* gives valuable pointers to detailed aspects that need investigation. The most critical
1737 data for the nutrient resource limitation hypothesis would be phosphorus concentrations in
1738 roots, branches, leaves and fruits of a large sample of trees over several masting cycles.

Detection of phytic acid in branch wood, prior to fruiting especially, could confirm that P was being stored. Lack of predicted changes in P over time would falsify the hypothesis. In addition, to test the related economy-of-scale mechanism for equilibration of P between adult trees at masting would require showing everywhere a flux of P through the mycelia of the shared ECM network, i.e. between neighbouring large trees.

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

Acknowledgements

We thank Sylvanos Ngibili (phenological recording) and Marlise Zimmermann (chemical analysis of plant and soil materials in Bern), both of late, for their valuable assistance. Xander van der Burgt helped with the soil moisture readings. The beginning of the second phase of the mast fruiting recording was supported by Swiss National Fond Grant #3100-066655 (2002–2006): all subsequent costs were then met by the Chair of Vegetation Ecology (DMN), University of Bern. The Ministries of Forests and Wildlife (MINFOF) and Scientific

Research and Innovation (MINRESI) granted permission to conduct the research, and the Conservator's Office of Korup National Park provided access to the site.

Author Contributions

DMN conceived and led the research, wrote the first full draft of the paper, developed the hypotheses, and performed the statistical analyses. GBC and CEE contributed to the climate data collection and instrument calibrations, and CEE provided access to the oil palm yield data. GAN and JMN provided information and analysis of the herbivore events. SS provided data and input on the nutrient estimates. MW undertook the tree coring and stem increment measurements. GBC, GAN, SS and JMN all at different stages assisted with phenology recording. All coauthors commented and approved the final draft on the paper.

Competing Interests: None.

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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: mean daily (a) rainfall and (b) 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 Appendix 5: Fig. S1).

2281 Fig. 4. Changes in the mean scores of five phenological stages of *M. bisulcata* trees at Korup
2282 in (a) 2009-2010 and (b) 2011-2012. Stages: leaf fall (blue), leaf flush (purple), flowering
2283 (green); immature (yellow) and mature (red) pods. The horizontal red lines indicate the span
2284 of the dry season for each year (see also Appendix 5: Fig. S2).

2285 Fig. 5. A schematic flow diagram of the interrelated hypothetical processes behind mast
2286 fruiting (M) in the grove-forming population of *Microberlinia bisulcata* at Korup. The boxes
2287 with light blue shading are either empirically established, or at least can be very strongly
2288 inferred. They involve the deterministic factors soil phosphorus (P) and potassium (K), and
2289 the stochastic effects of dry-season (DS) rainfall. Those in grey concern radiation and carbon
2290 (C)-supply, dynamics and allocation. The box in pale brown-orange concerns the likely
2291 important role of ECM networks and nutrient fluxes within the root mat, which are
2292 hypothetical and require empirical confirmation. The central double-headed arrow represents
2293 the interplay between within-tree and between-tree processes. Green shading and lines
2294 indicate the proposed threshold triggering flowering and fruiting, and repeated annual uptake
2295 and storage over successive years within the masting cycle of typically 2-3 years. Hormonal
2296 control of masting, shown in yellow, is strongly suspected: it also requires critical testing.
2297 The small polygon in lilac, centre-left, is the primary condition for mast fruiting to occur, as
2298 shown by statistical model fitting in this paper (t is time in years). It is the process-link
2299 between the start and end of the diagram. Changes in the degree with which flowering results
2300 in fruiting, and in the intensity of fruiting itself (e.g. when lowered to 'm'), are explained in
2301 the main text.

2302

List of Appendices

1. Radiometry at Bulu, Ndian: calibration and interpretation.
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7. Analysis of Ndian PAMOL oil-palm plantation yields.
8. Stem increments from tree stem cores.

Data availability statement:

Open Research Statement. Data files for 'private-for-peer reviews are found at:

https://datadryad.org/stash/share/4KTFQYuroW0ctbSd5_Y9lSswTWfmD5Glkj3EGf_w_MI

Newbery, D. M., et al. (2023), Data from: Mast fruiting in a large tropical African legume tree provides evidence for the nutrient resource limitation hypothesis, Dryad, Dataset, https://doi.org/10.5061/dryad.r7sqv9shz

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

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

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

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

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

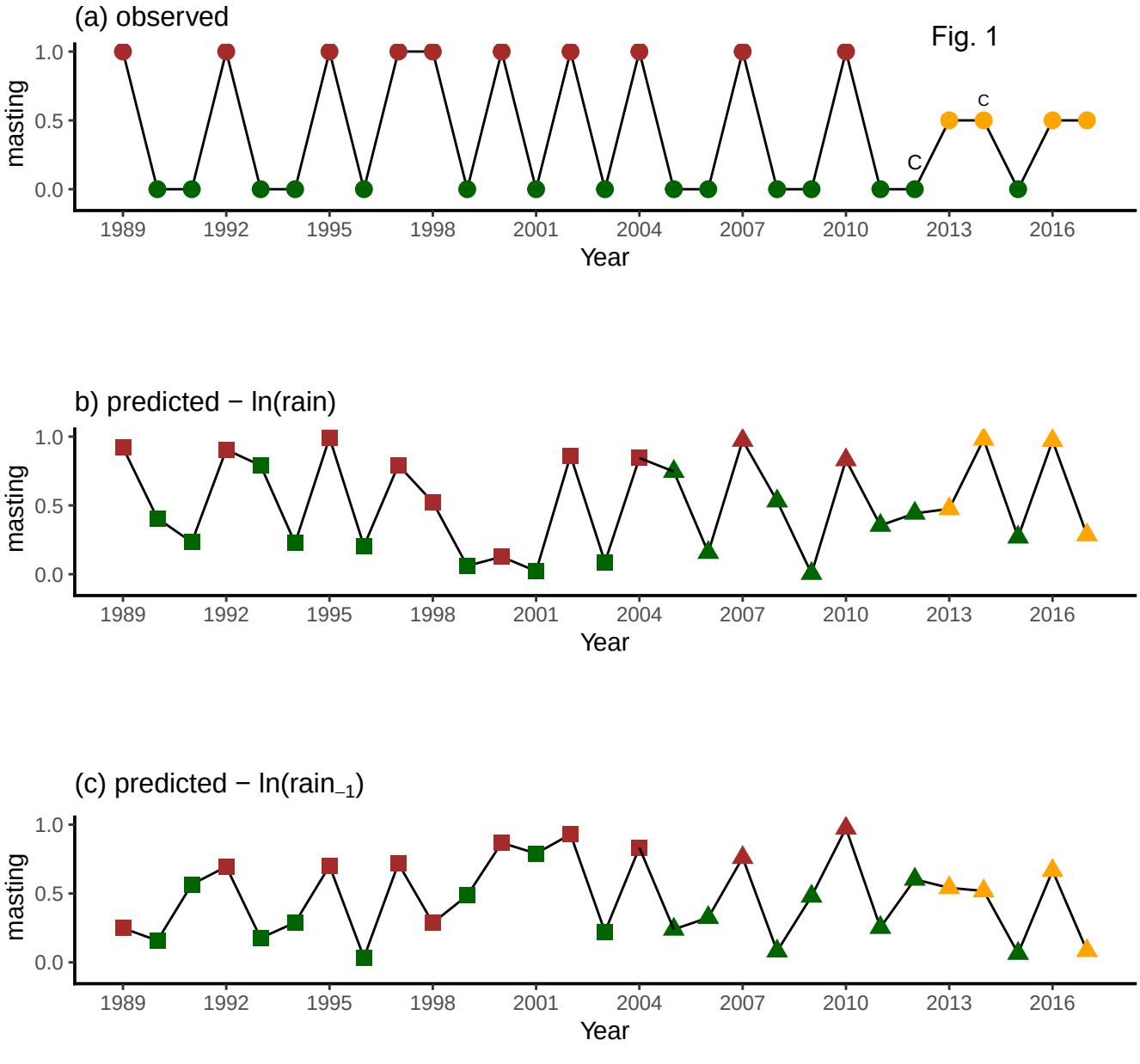
$t_{>mast}$ (n)	year	N	P	Ca	K	Mg
1 (30)	2011	16.06 ± 0.25	0.597 ± 0.018	14.71 ± 0.58	4.41 ± 0.11	3.40 ± 0.13
1 (20)	2002[a]	17.39 ± 0.33	0.632 ± 0.026	NA	5.58 ± 0.45	3.43 ± 0.17
2 (5)	1991[b]	15.72 ± 0.66	0.692 ± 0.025	13.99 ± 0.82	4.67 ± 0.23	3.89 ± 0.17
3 (5)	1992[b]	19.33 ± 0.55	0.809 ± 0.047	12.70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

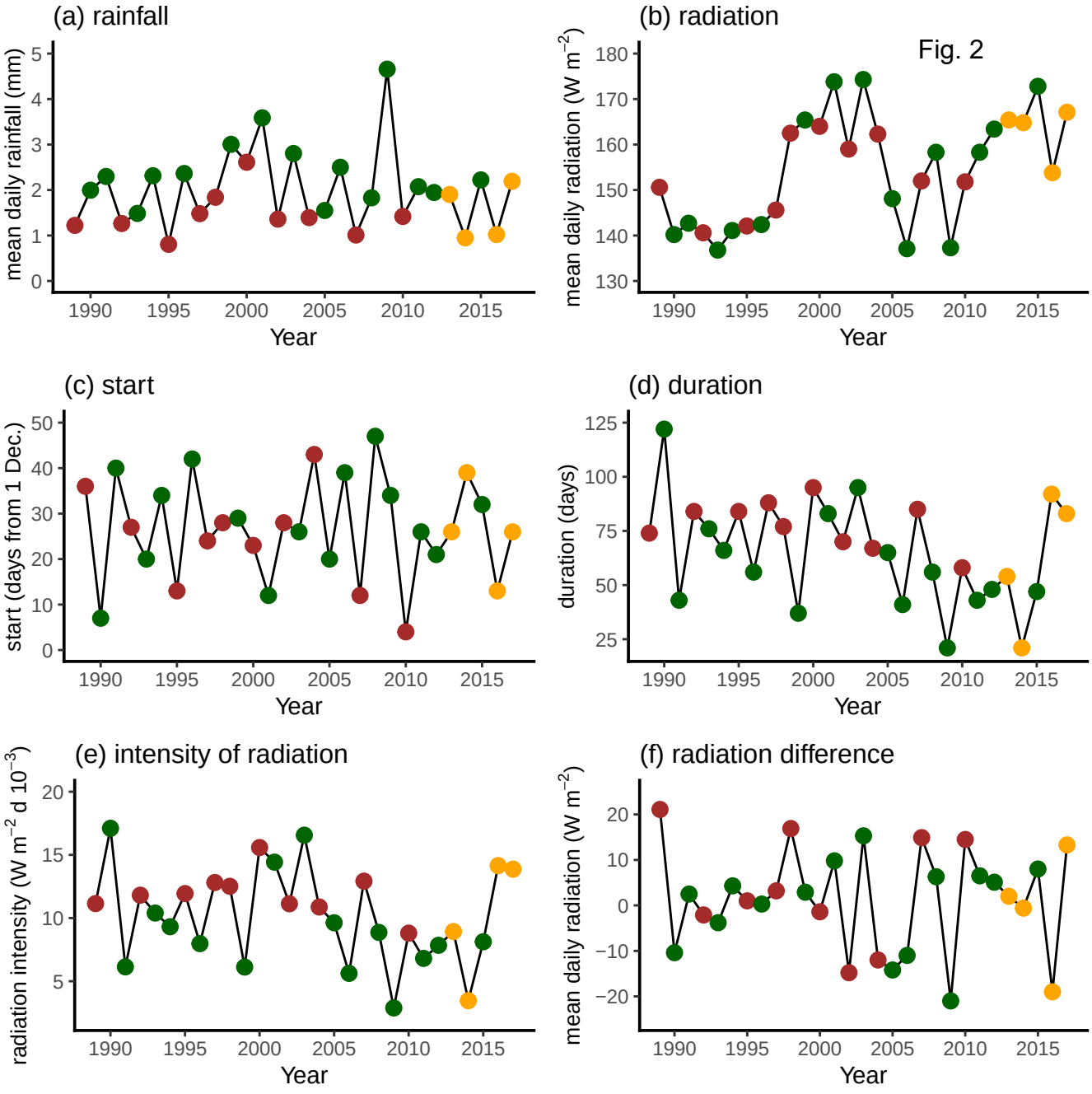
[a], Schwan (2003); [b], Chuyong (1994) and Chuyong et al. (2000).

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

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

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


(a) observed
Fig. 1
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

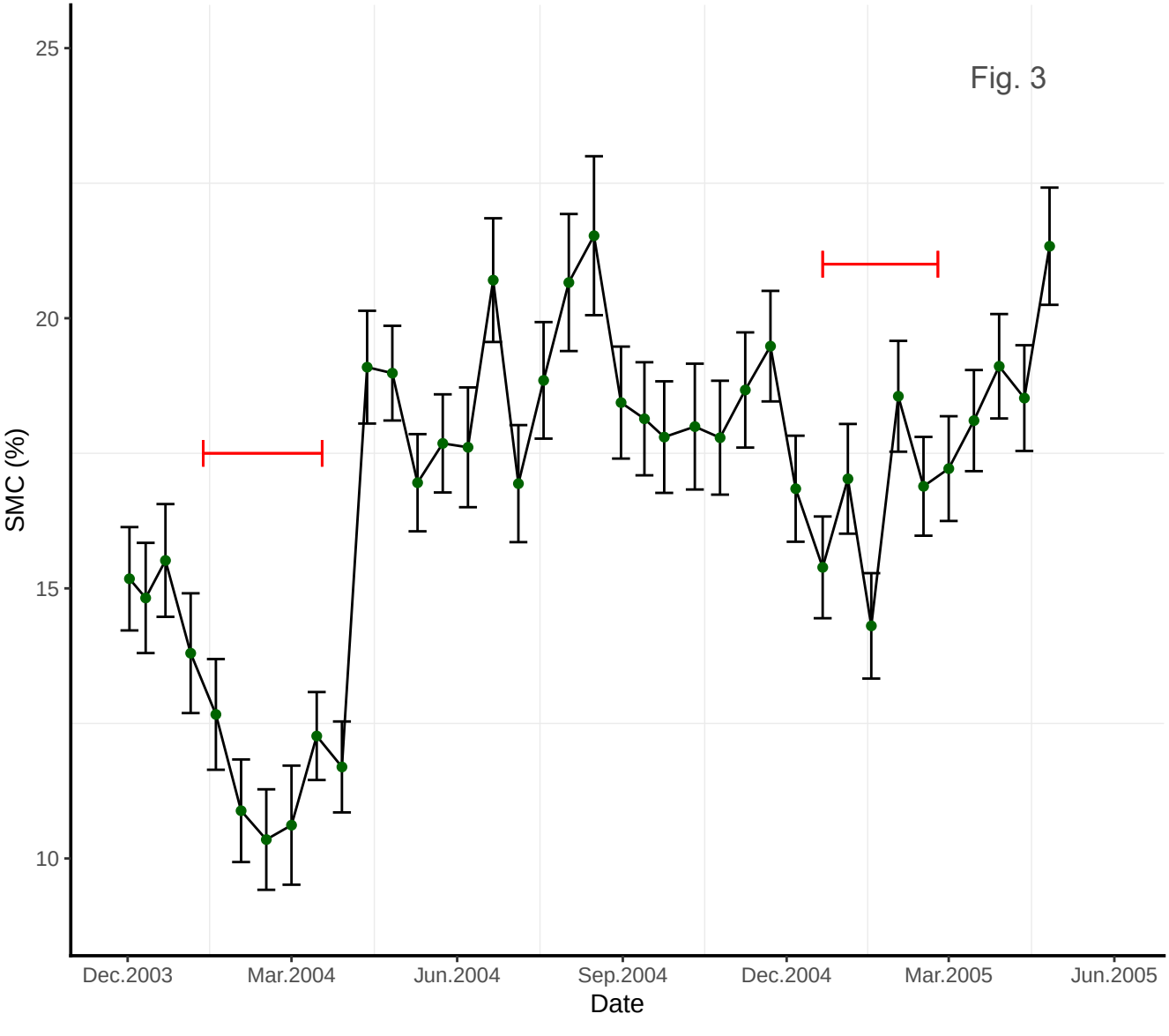


Fig. 3
SMC (%)
25
20
15
10
Dec.2003
Mar.2004
Jun.2004
Sep.2004
Dec.2004
Mar.2005
Jun.2005
Date

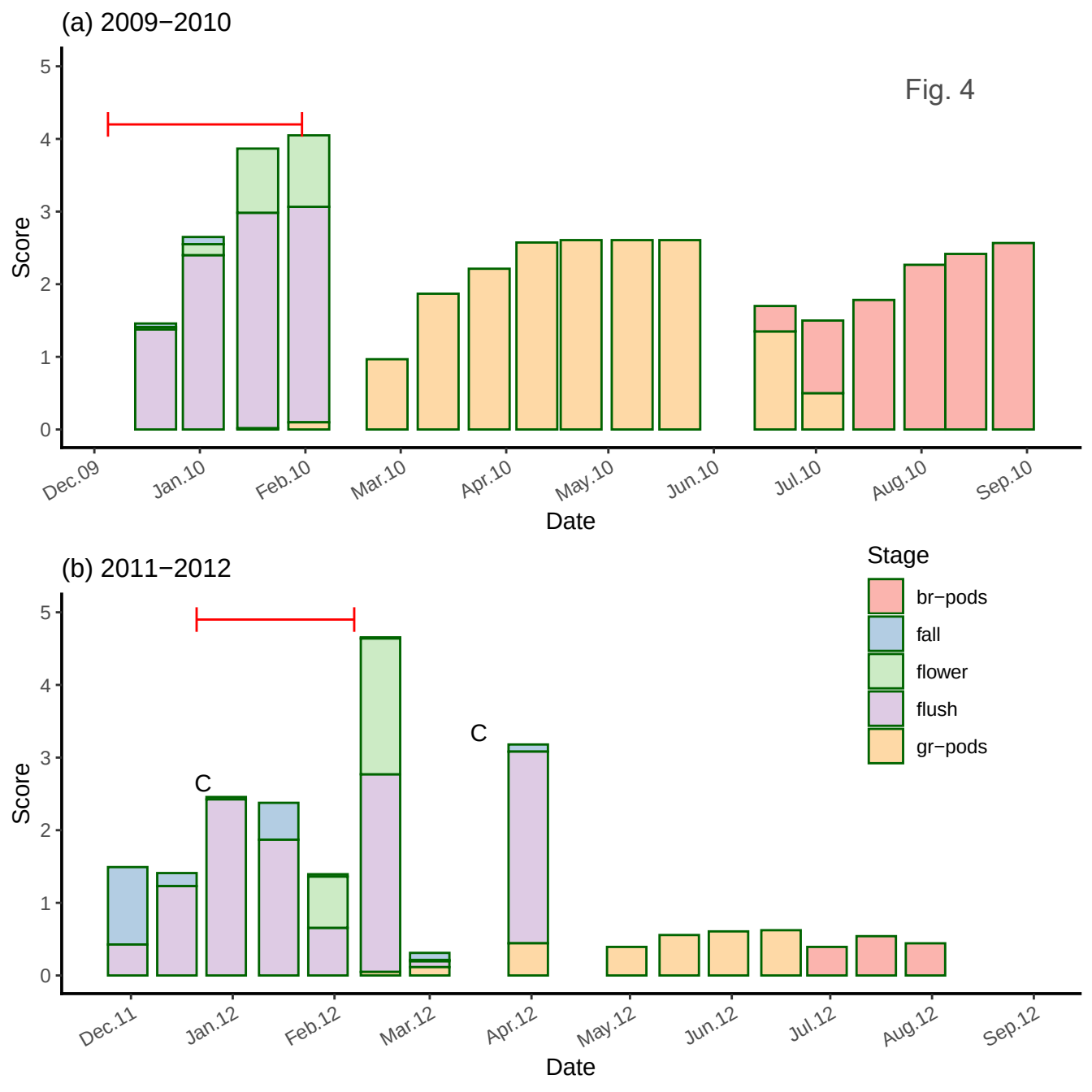
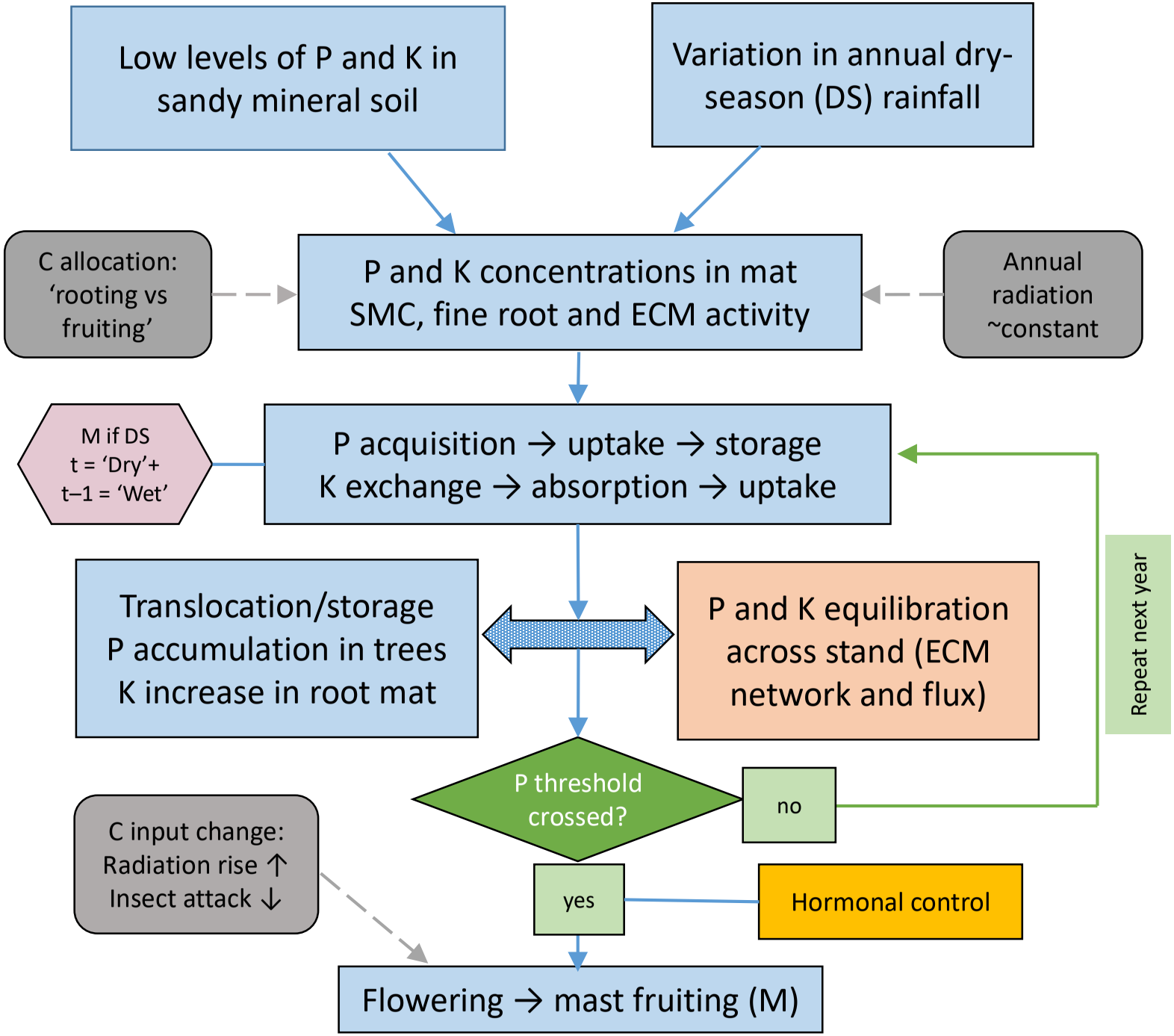

(a) 2009−2010
Fig. 4
Score
0
1
2
3
4
5
Dec.09
Jan.10
Feb.10
Mar.10
Apr.10
May.10
Jun.10
Jul.10
Aug.10
Sep.10
Date
(b) 2011−2012
C
C
Score
0
1
2
3
4
5
Dec.11
Jan.12
Feb.12
Mar.12
Apr.12
May.12
Jun.12
Jul.12
Aug.12
Sep.12
Date
Stage
br−pods
fall
flower
flush
gr−pods

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)