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

David M. Newbery1*, Sarah Schwan1, George B. Chuyong2, Godlove A. Neba2, Culbertson E. Etta3, Julian M. Norghauer1,4, and Martin Worbes5

1 Section for Vegetation Ecology, Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland
2 Department of Plant Science, University of Buea, POB 63, Buea, South West Region, Cameroon
3 Research and Development Section, PAMOL Plantations Plc, Lobe Oil Palm Estate, PMB 3, Ekondo Titi, South West Region, Cameroon.
4 Present address: Statistical Scientific Editing, Montréal, Québec, Canada
5 Tropical Plant Production and Agricultural Systems Modelling, Georg-August-University, Grisebachstraße 6, DE-37077 Göttingen, Germany

* Corresponding author david.newbery@unibe.ch

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Abstract

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

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

**INTRODUCTION**

By fruiting and seeding intensively at intervals as opposed to continuously over the years,
seed and seedling survival may be enhanced for plants species with a masting iteroparous type of
life-history (Charlesworth 1980, Stearns 1992). Trees provide the large majority of the
documented cases. To explain how a species’ fitness can be maintained or increased, a so-called
‘economy of scale’ concept has often been invoked. Three general processes have been proposed
to achieve this economy, usually thought of as the teleonomic causes of mast fruiting and
seeding: (1) the efficacy of fertilization may be increased by mass flowering, (2) seed predation
may be more readily satiated by mass seeding, and (3) the chances of successful dispersal and
establishment may be improved by larger reproductive output. The three processes are not
mutually exclusive, they can happen together to different degrees and different times, and they
could involve non-linear interactions. A model of an evolutionary stable strategy (*sensu* Maynard
Smith 1972) for masting appears not to have been worked out so far: a suitable conceptual
starting point could be the hypothesis of a serial adjustment of reproductive investment of Lloyd
(1980).
Stochastic variation in weather conditions from year-to-year, interacting with site
substrate conditions, very likely also play important moderating roles in masting. Kelly (1994),
Kelly and Sork (2002), Crone and Rapp (2014) and Pearse et al. (2016) provide reviews of the
now extensive literature in this field of study, covering the key concepts and hypotheses for
masting. Much of the research reported has been in the ecological and evolutionary direction
with a distinctly temperate-biome emphasis (e.g. for oaks, Koenig and Knops 2000). Beyond the
dipterocarps in SE Asia (e.g. Curran and Leighton 2000), other studies in the tropics have been
very few. More critical is that there still remains a basic lack of understanding of the underlying
tree physiological mechanisms which enable mast fruiting and seeding to operate within an
ecosystem. Together with the relevant environmental conditions, these mechanisms are
sometimes referred to as proximate causes. What are viewed as proximate causes might in fact
be the teleonomic ones as well.

For flower, fruit and seed production during a masting year to be allocated efficiently
over the life-time of the adult tree, a physiological resource-mechanism must at least be in place.
Budget models initiated by Isagi et al. (1997) have simulated how a resource, usually carbon (C),
accumulates in storage to an internal plant threshold which then triggers flowering. Almost all
such models have involved the coupled wind pollination of individuals (Abe et al. 2016, Satake
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
et al. 2013, Sanchez-Humanes et al. 2011, Würth et al. 2005). Macronutrients have been
suggested as potential key resources underlying budget mechanisms from just a few studies, but
the evidence is scarce because this topic has been so little researched. Han et al. (2014) and Han
and Kabeya (2017), for example, have shown that nitrogen (N) storage and mobilization is
important for triggering flowering; and Fernandez-Martinez et al. (2017b) that P and Zn are
likely involved in the mast fruiting of temperate forests. Carbon however should not be laid aside
completely as a candidate resource as it likely operates in concert with N, phosphorus (P),
potassium (K) or other elements, not just to build fruits and seeds but indirectly to grow and
maintain other organs like roots for nutrient acquisition.

If macronutrients are behind the mechanisms of mast fruiting it would be expected that
the element most important in control might be the one which is at lowest level of availability at
the site, being that in most critical supply overall (Allen et al. 2017, Fernandez-Martinez et al.
2019). It will need to be accumulated to support reproduction, which in turn depends of attaining
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. This appears to be an extension
of Liebig’s Law. 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-
such-low supplies, suggests a nested system of storage and thresholds with a similar structure.
Even so, the particular nutrient(s) could probably be different for different species, habitats and
biomes. The search then is for the key element(s) most determining growth rate of the trees and
controlling nutrient cycling, which then explain 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 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 hypothesis therefore stands that nutrients lie behind mast fruiting at the mechanistic,
tree-physiological, proximate level, and for many species, in particular species that are
ectomycorrhizal (Fagaceae, Pinaceae, Caesalpiniaceae, Dipterocarpaceae, etc.). It is testable and falsifiable. Ectomycorrhizas (ECMs) may enable a form of economy of scale due to their large shared mycorrhizal networks between tree roots equilibrating the levels of the limiting nutrient resources (Newbery et al. 1998, 2006a). Both the tropical dipterocarps and caesalps are strongly ectomycorrhizal and, more generally, masting in most temperate and tropical species is strongly associated with having this symbiotic mode at the genus/family level (Newbery 2005). The role of ECMs has been importantly overlooked in discussions of the causes of mast fruiting, especially at the operating level of proximate factors (Corrales et al. 2018). A prime example of a tropical ectomycorrhizal caesalpinaceous species which also shows strong mast fruiting is *Dicymbe corymbosa* from Guyana (Henkel et al. 2005, Henkel and Major 2019). This and the work of Green and Newbery (2002) and Newbery et al. (2006a) in a related study of *Microberlinia bisulcata* in Cameroon were not considered by Pearse et al. (2016) though. Outside of the impressive mass flowering events of the Dipterocarpaceae in SE Asia (see Chechina and Hamman 2019), mast fruiting in the tropics has barely been recognized (Norden et al. 2007).

There is a further aspect when considering how resources may affect reproductive investment and schedules. In many cases, with the large dry mass allocations in masting events, C is certainly involved, but it may not be a determining resource as regards reproductive timing. Such high demands will mean that less C is available for root growth and root replacement, and for stem and branch growth and maintenance, once the other key nutrient accumulated has initiated the switch to fruiting (Kozlowski 1971). Accordingly, a secondary hypothesis advanced further in the present paper, is that C is allocated more to these other tree parts in the interval years between mastings. It will assist in nutrient acquisition in the case of roots, and in building
new wood and bark storage cells in the case of stems and branches, in preparation for the next
mastig. This is not to say that C and N (and K or other elements) would not be accumulated in
the interval as well, but the accumulation of the more limiting (or controlling) element, say P in
the case of caesalps, would probably be critical to the triggering. It would ensure that the
elements are supplied in the stoichiometric proportions needed for the tree as a whole to move
forward to successful fruiting.

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

**BACKGROUND AND CONTEXT**

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

*Microberlinia bisulcata* dominates large patches or ‘groves’, 1-3 km across, in the
primary rain forest of southern Korup. Trees ≥ 50 cm stem diameter attained 17.8% of the
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, acidic
and very low in available P and K (Gartlan et al. 1986), meaning that here high-stature tropical
forest is growing on one of the nutrient-poorest sites in tropical Africa. Within groves, soil
organic matter is largely confined to the top 2 cm of the profile, forming a surface mat that is
densely occupied by fine roots and mycorrhizal hyphae (Newbery et al. 1988, 1997). Larger vertical roots are able to tap deeper water reserves. Nutrient cycling in the groves shows a ‘fast-forward’ modus: leaf litter decay is fast, there is no permanent leaf litter layer, and most cycling via the very efficient mat happens in the early wet season (Chuyong et al. 2000, 2002). At this time throughfall nutrients help to prime decomposition and uptake (Chuyong et al. 2004). For the rest of the year, heavy rains leach the forest, and this results in a tight closed ecosystem in which ECMs play a central role in P acquisition and uptake (Newbery et al. 1997). In addition, annually in the dry season, Harmattan dusts bring some P to the forest by aerial deposition. A critical field experiment showed that growth and recruitment of *M. bisulcata* was not P-limited (Newbery et al. 2002), presumably because of the highly evolved adaptations to the low-phosphorus site.

Recruitment of *M. bisulcata* over at least the last six decades has been poor due to very low seedling and sapling survival (Newbery et al. 1998, 2000, 2006b, 2010; Norghauer and Newbery 2010). Seed production in mast years is copious (Newbery et al. 2006a) but this species’ seedlings are strongly shade-intolerant (Green and Newbery 2001a, b). The groves demonstrate transient dominance: the stands now are predominantly made up of large to very large trees, with extremely few small ones present (Newbery et al. 2013). The dynamics is thought to be one of patches arising and then decaying, being replaced, *in situ* or *ex situ*, within a mosaic of species-richer forest (Newbery et al. 2013, Newbery and Gartlan 1996). The species is classified as a long-lived light-demanding tree (see Newbery et al. 2010). Part of the expected life-history strategy of long-lived and light responsive species such as *M. bisulcata* (Newbery et al. 2010) would be to delay the size on maturity (SOM) in order that greater seed output later offsets the relatively low probability of persistence in the forest understorey. Two further coevolved traits are ectomycorrhizal habit and mast fruiting. Ectomycorrhizas not only provide
advantages in resource acquisition for juvenile and young adult trees but are also thought to be a means to store resources which enable mast fruiting in the older adult ones (Newbery et al. 1998; Newbery et al. 2006a). A key hypothesis is that these links, and possibly also root grafts, between adults synchronize the timing of masts by equilibrating nutrient sinks across groves (Newbery et al. 2000, 2010). There is increasing evidence from other forests that ectomycorrhizas build intricate below-ground hyphal networks between individual trees (e.g. Simard et al. 2012, Simard and Durall 2004).

*Patterns in time and first hypotheses*

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

The climate at Korup varies stochastically from year to year, particularly regarding the
start, duration and intensity of the dry season (the dates defining the actual season each year
based on 30-day running rainfall total (rfi) falling < 100 mm; Newbery et al. 2006a). This season
plus the first six weeks of the wet season very largely determine tree physiological processes for
the whole year. Fine-tuned sensing of the environment to optimize resource gain and allocation
within a life history strategy is central to survival. Under- or over-allocation at the wrong time
could lead to large fitness losses, hence the presumed operation of thresholds that safely trigger
phenological change. That C and P might be dual constraints within a broader nutrient-limitation
hypothesis as an explanation of mast fruiting for many tree species required a detailed budget to
show how much C and P (also N and K) were being allocated to fruits and seeds in a main
masting event. Censuses of seed and pod counts, their masses and nutrient contents were
achieved for the 1995 masting (Green and Newbery 2002), showing that M. bisulcata produced
on average 26K seeds per tree or 83.5K seeds/ha. Seeds are small (0.64 g each), and with an
average of 2.0 seeds per pod, total pod mass was 25 g (see images in Norghauer and Newbery
(2015: Appendix S1; at the 2007 and 2010 events 2.5 seeds per pod were estimated). Masting
resulted in an investment of 1034 kg /ha dry mass that year, and compared with leaf litter
production in previous non-mast years (Chuyong et al. 2000), was 52% of it by comparison, or in
a mast year 74%, i.e. a substantial allocation of resources (Green and Newbery 2002). Seeds and
pods together had N and P amounts 13 and 21% of that in annual leaf litter production, indicating
an important use of P during masting. Unfortunately, C, P, N and K investments in flowers are
unknown but if included they would increase the reproductive allocation estimates slightly.

Flowers of *Microberlinia* are very small in mass compared with seeds and fruits.

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

The argument developed was that the current year’s dry season dryness reflected also to some degree increased radiation, but the wetter dry season the year prior was possibly indicating better conditions promoting tree nutrient uptake at the most effective time. The detailed phenology data showed that masting was strongest on trees on upper slopes (i.e. sites with relatively drier surface soils in years with a ‘dry’ dry-season), and that in the moderately ‘wet’ dry season of 2000, those trees that masted were also on the drier sites. This tentatively pointed to surface soil moisture in the dry season being a key determinant to what was happening. The intensity of the dry season is unlikely to have particularly affected the water balance of adult trees themselves because they would have had access to deeper water sources: after all, trees
flushed, leaves and branches grew, and flowering took place, in the dry season. Taken together,
the preliminary evidence pointed to processes in the organic mat regarding fine roots and ECMs,
coupled to nutrient transfers within the trees and ectomycorrhizal network (Newbery 2005,
Newbery et al. 2006a). With the masting time series extended to 29 years—almost twice its
previous length, plus information collated from several nutrient studies at the site, further tree
phenology censuses, a more detailed statistical modelling of fruiting on rainfall and radiation,
and the effects of an unexpected herbivore attack—this paper assesses the extent to which C, P
and K, might be determining the masting cycle in *M. bisulcata* and, *in extensio*, presents a more
refined hypothesis and model of this remarkable phenomenon.

**METHODS**

**Location**

Korup National Park, in the South-West Region of Cameroon, is covered by primary rain
forest of the Atlantic Coastal type (Letouzey 1968), and lies within the Guinea-Congolean
refugium (Gartlan 1992). Phenological recordings were made in the main ‘P-plot’ located in the
southern part of the Park (5°10’ N, 8°70’ E) at an elevation of c. 100 m a.s.l. (see Newbery et al.
2004, 2013). Mean rainfall 1984-2016 was 5159 mm (range 4023 to 6531). Access to the
neighbouring oil palm estates of PAMOL Plc outside of the Park (Bulu-Mundemba, Ndian)
allowed a comparison of their fruit yield with *M. bisulcata* mast fruiting with regard to climate
variation. The estates have the same substrate and soil type as southern Korup but have received
phosphate fertilization for several decades.
Climate

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

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

Phenology

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

To increase the frequency of recording, between 1995 and 2000, 150 M. bisulcata trees in
the main 82.5 ha ‘P-plot’ (out of 294 in total with stem diameter ≥ 50 cm; Newbery et al. 2013)
had been scored on 61 occasions (mostly at monthly intervals), for intensity of leaf fall, leaf
flush, flowering and immature and mature pods (scale 0-3; Newbery et al. 2006a). Later, now within an 8-ha sub-area of the 82.5-ha P-plot (1000-1200 m E, and 100-500 N, with respect to SW origin; see Fig. 2a of Newbery et al. 2013), 61 of the 65 trees surviving since the last enumeration in 2005 (stem diameter, mean ± SE = 112 ± 4 cm, range = 54 – 174 cm), were scored between 2009 and 2013 in a similar manner as the first period. In 2014, fallen pod density on the ground was taken as a proxy for mature pod density (Appendix 2, Table S1).

**Nutrients**

In an earlier litterfall study between May 1990 and June 1992, monthly bulked samples from twenty 40 x 40-cm traps in each of 10 subplots were divided into two halves as set A, for separation into fractions (leaves, small wood, etc.), and set B, for separation of just leaves into the commonest 26 species (Chuyong et al. 2000). From this set B, leaves of *Microberlinia bisulcata* were selectable and later – as for the other species – they were analyzed for N, P, Ca, K and Mg concentrations. Leaflets and rachises were kept together. This species is a leaf-exchanger, and has a very well-defined period of leaf litterfall annually, starting with onset of the dry season (Newbery et al. 2006a). Subplots (each 40 x 80 m), were composed of five in low (LEM) and five in high (HEM) ectomycorrhizal stands along the transect P in Korup (Gartlan et al. 1986, Newbery et al. 1997). *Microberlinia bisulcata* occurred in only the HEM subplots, so the number of replicate nutrient values per month was five. The 26 months were divided into seasons according to the median rainfall pattern at Korup (as defined above), with those in the dry season being generally December 1990 – February 1991 and December 1991 – February 1992, and the other months the longer wet seasons. Only dry seasons are considered here, and nutrient concentrations for them were averaged across the three constituent months. A mast fruiting occurred in (August-September) 1989, so dry season 1990-1991 is the second dry season.
after the event, and dry season 1991-1992 the third one. The next masting was in the wet season
of 1992, so seen from this perspective the two dry seasons sampled were ~ 6 and 18 months prior
to the second event.

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

In the dry season 1997-98 four traps of galvanized metal (same as used in 1990-92) were
compared with four similar ones but with hessian sack linings (used in the 1989-1991 study of
Newbery et al. 1997), each set being placed at random in each of the two quarter plots of six
HEM half-plots. Litter was collected over four consecutive fortnights between 21 December
1997 to 15 February 1998. *Microberlinia bisulcata* leaflets and rachises were again sampled
separately, dried and analyzed for N and P concentrations. Not all traps had sufficient material
and the replication per subplot/trap type/date ranged from 2 to 4. N and P values were successive
averaged for trap type, then subplot, and their weighted 4:1 leaflet-rachis averages found for the
24 date x plot combinations. Trap type had no effect on these two elements’ litter concentrations (testing for Zn contamination had been otherwise intended). This litterfall was collected midway between a moderate double masting in wet seasons 1997 and 1998.

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

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

Soil moisture

Soil moisture was recorded across two dry seasons to show that its variation could underpin soil nutrient processes which might be affecting mast fruiting, given also that M.
bisulcata trees have such very extensive lateral root systems close to the soil surface (Newbery et al. 1997, 2009). 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 opportunistic 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

If masting is driven by availability of resources, and these are partly stochastic and partly trending over time, then a full range of possibilities for interval length can be accommodated for M. bisulcata. The extended time series (Fig. 1) shows that after 1995, as radiation increased (Table 1), 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 had moderate masting fruiting. The time series as it extended began to show increased non-stationarity, the first-detected period of 3-year cycling of 1989-1995 returned only once in 2004-2010: the regular cycle was seemingly just temporarily disturbed. Nevertheless, ‘on average’ over the 29 years, and taking as markers the first of those pairs of years with partial masting (2013, 2016), there appears to be good evidence of an intrinsic 3-year cycle. Because the time series is evidently non-stationary, any tests of randomization using techniques such as bootstrapping will not provide valid inferences (Cox 1981). Furthermore, bimodality will not be detected if the interval varies between 0 and 2 years.

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

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

Mean daily dry-season rainfall in years of full masting was lower than in those years’ prior with no masting (Fig. 2a), with the exception of 2000, and if the averages of the rainfall values for the two double partial masting years are taken these are on a par with the masting ones. The time series for rainfall showed weak temporal autocorrelation (Appendix 3: Fig. S3a), and likewise albeit a little more strongly for ln(rain) at lag 1 (−0.293 vs. −0.221). (Note that the first correlation differs slightly from the rain versus rain_{−1} one based on data which included the lagged 1988-value.) Radiation over time showed a distinctive pattern with a clear central peak between 1996 and 2005, then a rise again, apart from 2009, to those higher levels (Fig. 2b):
accordingly, the series evidenced non-stationarity, and as a consequence autocorrelation was positive and significant for lags of 1 and 2 years, then significantly negative \((P < 0.05)\) for lags of 6-8 years (Appendix 3: Fig. S3b).

Start of the dry season varied around the third to fourth week of December with no clear patterns or differences between masting and non-masting years (Fig. 2c), but it was negatively autocorrelated with a lag of 1 year, i.e. early starts tended to be followed by late ones, then early again, in successive years (Appendix 3: Fig. S3c). Excepting the two last years, duration of the dry season revealed a general decline (an approximate halving), those years with masting being often longer, and conversely of the six shortest-season years there was no masting, apart from 2014 which was partial (Fig. 2d). Interesting, autocorrelation of duration was almost just significant \((P < 0.05)\) at a lag of 3 years (Appendix 3: Fig. S3d). Radiation intensity showed a very similar pattern to duration (since radiation varied much less than duration) (Fig. 2e; Appendix 3: Fig. S3e). Intensity of radiation in the dry season was expressed as mean daily radiation x duration. Lastly difference in radiation \((\text{radid})\) 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 \(\ln(\text{rain})\) and \(\ln(\text{rain}_{-1})\) improved the regressions fits with \(P < 0.015\) (Appendix 4: Table S1). Mean daily rainfall was only weakly correlated with rainfall the year prior, untransformed values \((r = -0.190, P = 0.374)\), transformed
(\(r = -0.272, P = 0.15\)). This last result is important because a strong negative temporal
autocorrelation, i.e. a year-to-year increase-decrease reversal, was absent. Regressions with both
rainfall terms led to reduced fitting, because these coefficients were now partial ones adjusting
for the correlation (\(P = 0.093\) and \(0.055\)). The same with ln-transformed variables also changed
the significance levels very little (\(P < 0.10\); Appendix 4: Table S1). Ordinal logistic regressions
improved the fitting further with the full 1989-2017 data. Concentrating on the models using ln-
transformed variables, separate regressions were now more, and highly, significant (\(P < 0.01\)),
coefficients with the same signs as for the simpler binomial logistic ones (Appendix 4: Table S1
and Fig. S1) and, whilst significance decreased again using two-term models, they were still
relatively strongly significant overall (\(P < 0.025\)).

The mean difference in ln-transformed dry-season mean daily rainfall, ln(rain), between
the current masting (t_0) and year prior (t_1) was highly significant (\(P < 0.005\)), but much weaker
for the same and penultimate year (t_2) (\(P = 0.15\)). Back-transformed means were 1.37, 2.49 and
1.69 mm/day respectively (see Appendix 4: Table S2). Comparing rain at t_0 with means of rain
at t_1 and t_2—applying equal or unequal weighting—led to very similar results as those at t_1
alone (\(P < 0.005\)). As a robustness test of the ‘M’/‘m’-grading of mast fruiting, and how that
might have affected the relationship with mean daily rainfall in the dry season, where there was
some uncertainty in the final grading, 1989-2017 ordinal logistic regressions were rerun with the
‘M’ for 1998 and 2000 replaced by ‘m’, i.e. 1.0 by 0.5. The dependence of masting on ln(rain) in
the current and prior seasons became slightly stronger (\(t = -3.209, P = 0.0036; t = 2.913, P =
0.0074\), respectively).

Mast fruiting showed no significant dependence on mean daily radiation in the drought-
defined dry season, in either the 1989-2012, or 1989-2017, time series (using binomial and
ordinal regression, respectively), for the current \((\text{radi}; P = 0.72 \text{ and } 0.80)\) or prior \((\text{radi}-1; P = 0.55 \text{ and } 0.62)\) seasons. Correspondingly, start date was also a poor predictor of masting for the current \((\text{start}; P = 0.34 \text{ and } 0.29)\) or prior \((\text{start}-1; P = 0.18 \text{ and } 0.27)\) seasons. Duration, although only weakly significant, was better for the current \((\text{dur}; P = 0.080 \text{ and } 0.095)\) or prior \((\text{dur}-1; P = 0.071 \text{ and } 0.138)\) 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, \(P = 0.083 \text{ and } 0.097\); ordinal logistic, \(P = 0.096 \text{ and } 0.165\)). 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, \(\text{radi}_d\)), on the drought-defined dry-season basis, had no clear effect on masting (binomial logistic, \(P = 0.31\); ordinal logistic \(P = 0.84\)).

Radiation showed a distinctive long-term trend since the start of recording until 2017 (Appendix 3: Fig. S2), with the evident 11-year cycle. This was not related to change in instrumentation at Bulu (Appendix 1). Using a LOWESS regression fitting model in R (‘lowess’ command—a set of local smoothing splines, this trend could be removed and the differences between empirical measurements and the detrending curve then used as adjusted local year-to-year changes Appendix 3: Fig. S2a). The best result was with a span parameter of \(f = 0.25\), which meant that radiation values > 1 year prior or ahead had some weight in fitting values for any one year, which simple differences between successive years did not. Binomial (1989-2012) and ordinal (1989-2017) logistic regression fits of masting to drought-defined dry-season \(\text{radi}\) and \(\text{radi}-1\) were, however, all clearly insignificant \((P = 0.34 \text{ to } 1.00)\).
Lastly, to check whether heavy showers early in the dry season may have damaged flowers or interfered with pollination success, mean daily rainfall was plotted across each year’s season. Of the 14 years with strong (‘M’) or moderate (‘m’) mast fruiting, ten had no showers of ≥ 15 mm/day in the first 30 days, whilst in the 15 years without mast fruiting eight had no showers ($\chi^2 = 3.55$, df = 1, $P = 0.060$), suggesting only a marginal tendency for mast years not to have experienced potentially destructive rainfall events.

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

Model predictions

Using binomial logistic regressions of masting 1989-2004 on ln($\text{rain}$) in the current and previous years, fitted models were used to predict masting in 2005-2017 (Fig. 3), on the original response scale of 0 to 1 ($\pi$; Agresti 2007). The series started at 1989, not 1987 as used in Newbery et al. (2006a); and autocorrelation was not incorporated (see ‘Time series analysis’ later though). The model fit for ln($\text{rain}$) was good for the mast years 1989, 1992, 1995 and 1997 (marginal for 1998), and good for 2002 and 2004, but it wrongly indicated a mast in 1993 and missed the mast in 2000 (Fig. 3a; fitted intercept $[\alpha] = 3.61 \pm 1.80$ and slope $[\beta] = -5.77 \pm 2.62$, $t = -2.206$, $P = 0.027$). Predictions of masting in 2007 and 2010 were very high ($\pi = 0.97$ and 0.83 respectively), and also that it did not occur in the intervening years. After 2012 though, one each
of the pairs of moderate (‘m’) masts was predicted as full (‘M’, π = 0.98 and 0.97). The predicted masting in 2005 (π = 0.75) was incorrect, however.

With the model fit for ln(rain–1), 1992, 1995, 1997, 2000 [cf. with ln(rain)], 2002 and 2004 were all well-fitting as mast years, but 1989 and 1998 were not: 2001 was fitted as a mast year wrongly (Fig. 3b; fitted α = −2.47 ± 1.40 and β = 3.96 ± 2.00, t = −1.98, P = 0.027). Again, the model exactly predicted the mast years 2007 and 2010 masts (π = 0.76 and 0.97 respectively), and it managed three of the four ‘m’ 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’ heavy masting
in 2014 and 2017 (as predicted by the binomial logistic regression for \( \ln(\text{rain}) \)) (Fig. 3a), 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’ (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 \( \ln(\text{rain}) \) and \( \ln(\text{rain}^{-1}) \) respectively, for both lags \( p = 1 \) and 2, (Appendix 4: Table S1). Regressions using the time-series logistic regression model for \( \text{radi} \), \( \text{radi}^{-1} \), \( \text{start} \) and \( \text{start}^{-1} \) 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 fructing on dry season rainfall appears to be limited to the current and previous (\( t^{-1} \)) years, because repeat runs replacing \( \text{rain}^{-1} \) with \( \text{rain}^{-2} \), 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 ($\text{rad}_d$) and percent change ($\text{rad}_{d\%}$) 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 $\text{radi}$ ($P = 0.051$), negatively though more marginally for $\text{radi}_1$ ($P < 0.1$) (Appendix 4: Table S3b and Fig. S3). Time-series logistic regressions improved the fits especially for $\text{radi}$ ($P < 0.02$), although only slightly for $\text{radi}_1$ ($P = 0.80$). Fits to detrended differences (1989-2017) with ordinal logistic regression were intermediate in significance to those with binomial and time-series logistic ones.
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 radiation 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 mastig and most of those below were non-masting, attesting \textit{inter alia} that raised radiation differences and deviations were associated with mast fruiting.

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

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

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 ($t = 1.40, 0.45, -0.68$ 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, 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. 4: it included the two dry seasons of 2004 and 2005, defined as
before as when \( rft \) fell \(< 100 \text{ mm} \). Mean SMC over the 1.4 years was \( 16.80 \pm 0.48\% \). Repeated
measures analysis of variance for six times within each of the two dry seasons (Fig. 4), using all
12 sensors’ values, indicated that differences in mean SMC at the 20-and 40-cm depths were
very small and insignificant: \( 10.98 \text{ vs } 10.69\% \) in 2003-04 and \( 16.20 \text{ vs } 15.89\% \) in 2004-05, \( P =
0.88 \text{ and } 0.89 \) respectively, \( df = 1,10 \). In a similar-length period in the late wet season 2004,
starting soon after the peaked occurrences that year, a small difference was evident but again it
was clearly not significant \( (20.20 \text{ vs } 18.13\%, \ df = 1, 10 ; \ P = 0.39) \). Interactions between depth
and time were all insignificant for all three short periods \( (P = 0.19 \text{ to } 0.36) \).

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

Between 2 December 2003 and 26 April 2005, SMC was related to 30-day running
rainfall total as follows: \( \text{SMC} = 14.4 + 0.0070 \cdot rft \left( R^2_{\text{adj}} = 40.5\% , \ F_{1,36} = 26.18 , \ P < 0.001 , n = 38 \right) \), inferring 14.4 \% at 0 mm, and 21.4\% at 1000 mm – the last \( rft \)-value being close to the June
2004 maximum of 995 mm. The difference in SMC between the very driest and wettest times of
the mast year was therefore only 7\% — for those assumed free-draining locations. SMC before
the dry season of 2006-07 was \( 20.7 \pm 0.10\% \), and declined sharply and almost linearly to \( 14.0 \pm
0.67% (n = 9 sensors), a difference of 6.7%. With the dry season that year lying within the span of SMC recording dates, this last value was likely very close, if not at, the 2007 SMC minimum. The mean value at 29 January 2011, a date also well into that year’s dry season was 16.2 ± 0.8% (n = 8, one sensor lost because its cable was chewed), a value close to that in the dry season of 2005 (Fig. 4).

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

Caterpillar attacks

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

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

**Tree phenology 2010 and 2012**

Tree phenology of *M. bisulcata* was compared between the heavy mast fruiting year of 2010, and the year of 2012 in which fruiting was very low (Fig. 5; Appendix 2: Table S1). Both time series covered the drought-defined dry season of that year, and followed changes in leaf-flush and leaf-fall (leaf exchange), and flowering, pod formation (green) and pod maturity (brown). Attaining continuous fortnightly scoring was not always feasible and each series has two gaps. Leaf flush likely began a little before the start of the time series recorded for 2010, i.e. earlier than December 2009 (Fig. 5a), but was adequately captured for 2012 (Fig. 5b). The bulk
of the leaf-flush happened within each year’s dry season, flowering well within it in 2010 but
coming at the end in 2012. Even though the sum of the flowering scores was similar in both
years, fertilization resulted in substantially more green and brown bods in 2010 than 2012 (Fig.
5a, b). Caterpillars were not seen in the other years between 2009 and 2013, notably not in 2010.

In 2010, green pods were apparent between 18 January and 3 July, that is for 5.5 months, with a
1-month overlap as they turned brown between 5 June and 28 August, over 2.5 months (Fig. 5a).

A similar time course was recorded in 2004 (Newbery et al. 2006a: Fig. 6), and likewise (for
green plus brown) in 1995 and 2000 (ibid. Fig. 5d). Interestingly the overall period of pod
formation was much shorter in the two back-back years of masting 1997 and 1998.

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

The presence of the black caterpillar in 2012 appears to have upset the smooth 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. 1), 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 \( (n = 33 \text{ trees}; \text{ Appendix 2}) \), 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 \( rfi \) 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. 5b). With an interval of ca. 14 days between phenology census recordings, it is difficult to say which came first; but the most likely explanation is the further dry period caused flushing and this promoted renewed feeding, possibly from a next cohort of caterpillars that year. The dry season 2009-2010 had also several dry days at a similar time but broken by a large wetting event (and there was no further flush after the dry season one). For comparison, the pattern of 2010-2012 shows the shorter, late-starting and not so intense, dry season for a typical non-masting year (Appendix 6: Fig. S2b).

_Palm-oil yield comparison_

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

_Stem increment growth from coring_

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

Linear mixed-effects models were run using \(\ln(incr)\) as the response variable, trees as
subjects (or ‘blocks’) and ± ‘M’ as the factor. A binomial logistic regression fit of masting versus
increment was not feasible as the power, with only seven events in the period, was low. There
were no significant differences for increment in either the current year (\(F = 0.79, df = 1, 279; P =
0.38\)), or in the year prior (\(F = 0.12, df = 1, 279, P = 0.72\): increments available for 1988), or in
the year after (\(F = 1.90, df = 1, 259, P = 0.17\)). Thus larger respectively smaller increments were
not associated with current mast fruiting, not (by inference) caused by it, 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 (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 radiation remained significantly positively correlated (\( r = 0.532, df = 13, P = 0.041 \)), partialling out radiation effect was of little avail in unravelling a fruiting-stem growth interaction.

Nutrients and masting

For 1997 and 1998, and for 2011, the leaflet-to-rachis ratio of N was 1.568 and 1.524, and correspondingly for P it was 1.344 and 1.274 respectively, with means of 1.546 and 1.309. For 1997 and 1998, and for 2011, the leaflet-to-rachis ratio of K was 0.540 and 1.686, it was striking how much higher was the K concentration in the rachises compared to leaflets.

In the 1990-92 litter sampling, the bulked samples each represented 0.320 ha of forest. In 2011, the trapping the bulked samples each represented 0.368 ha. This means that each nutrient value is similarly based on ~1/3 of a hectare, and the respective samples sizes of 5-and-9 versus 30 can be retained in statistical comparisons without needing to group the 2011 ones.

Likewise, the 1997-98 study used some of the same half-plots, and accordingly had the same scale as in 1990-92. Working with the typical masting cycle of 3 years shown by *M. bisulcata* at Korup over the period 1990-92 (Newbery et al., 1998, 2006), the three sampling dates together allow a series of immediately-after (2010-11), and (1990-91) and 2 (1991-92) years after (and thus also immediately before the next) masting events to be constructed. The two consecutive years are likely temporally correlated, but the time difference between them and 2011 is large. The further data from 1997-98 present an interesting comparison in that masting in 1990-92 litter sampling, the bulked samples each represented 0.320 ha of forest.
1997 had evidently not prevented a repeat even the following year. Over the successive four fortights, concentrations of N were 18.69, 17.20, 18.58 and 18.63 mg g\(^{-1}\), and those of P were 0.802, 0.799, 0.787, 0.956 mg g\(^{-1}\).

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

The results show that in the inter-mast period, N was low for the first two dry seasons and then rose the year before the next masting, P increased from low to high approximately linearly in the period, Ca barely changed, K and Mg were relatively high for the first two seasons but fell in the third before masting (Table 2). This suggest that N and especially P concentrations were depleted by the last mast fruiting and were re-instated before the next event. K and Mg increased earlier in the interval but were presumably deployed elsewhere before masting. Despite the different sampling approaches, standard errors of means, across years per element, were quite similar. The concentration within the double-masting period 1997-98 intriguingly lay between the 1991 and 1992 ones for N, but were higher than both of them for P. That P was accumulating before masting is clearly demonstrated. The rise in P at the end of the litter fall series, but not of N, in 1998 is also remarkable (Table 2). The 1998 litter was collected immediately before a masting like the 1992 one, so they could be considered comparable in this respect even though
the previous mast fruiting events were 1 (unusually) and 3 years prior respectively. Averaging
the 2011 and 2002, and separately the 1992 and 1998, values where possible in Table 2 gives
composite estimates of leaf concentration respectively immediately post and prior to masting: N:
16.73, 18.80 (+12.4%), P: 0.615, 0.825 (+33.9%), K: 5.00, 2.44 (–51.1%), and Mg: 3.42, 2.53 (–
26.0%). These inter-mast changes suggest that N and P were depleted by fruiting and restored for
the next event—proportionally three-fold more for P than N, but the opposite occurred for K and
Mg.

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

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

Mast fruiting – a non-stationary process

If masting is driven by availability of resources, and these are partly stochastic and partly trending over time, then a range of interval lengths might be accommodated for *M. bisulcata*. In reality this range is limited to 1 to 3 years. The extended time series showed that between 1989 and 1995 there was a 3-year cycle, but after 1995, as radiation increased, there came a double year 1997-98 with high fruiting—1998 somewhat weaker than 1997, and then the cycle dropped to 2 years with a masting sequence 2000, 2002, and 2004, returning to very strong masting in 2007 and 2010 on a 3-year cycle, and finally after that the control seemingly weakened and resulted in two double-years, 2013-14 and 2016-17, which showed only moderate mast fruiting. Apart from being quite short at 29 years, the time series was non-stationary. There would be little reason to assume that it would a priori be stationary, especially, given the late transient cycle stage of the stand (Newbery et al. 2013) and the varying climatic variables on all time scales ranging from years to decades and centuries (Nicholson et al. 2000, 2018). The inconstancy might be best understood with a two- or three-factor threshold model, where C, P and K reach potentially different thresholds, simultaneously or sequentially. Thresholds themselves may not even be constant over time but relate to age, climate trends, and other tree-internal demands. When one of the resources reaches its threshold early, its effectiveness could be limited by the slower accumulation of another resource. The first resource will need to be stored or allocated elsewhere in the tree, even to then support the faster acquisition of the lagging resource. In time the second resource accumulates to a level that crosses a pre-set threshold, and this then allows the first resource to come into operation.
The allocations of C to mast fruiting in *M. bisulcata* are substantial. The earlier mast fruiting event of 1995, 28 out of 30 trees recorded had fruits. The average number of seeds per tree was ~26K (maximum 92K). Using estimates of mean dry masses of seeds and pods, and mean numbers of seeds per pod, the total dry mass investment was 17 and 307 kg per tree respectively, summing to 324 kg per tree (Green and Newbery 2002). These per-tree masses translate to 53 plus 981 = 1034 kg/ha, ~55% the mass of average annual leaf-fall (Green and Newbery 2002). Applying the individual seed and pod masses to counts made for the 2007 and 2010 events, for trees that had pods (Norghauer and Newbery 2015), gave 181 kg per tree in 2007 and 122 kg per tree in 2010. (Excluding the two zero-producers, output values for 1995 were 346 kg/tree.) On this basis the investments per masting tree in 2007 and 2010 were 52 and 35% respectively of that in 1995, illustrating an up to almost two-fold variation in masting intensity across these full fruiting events. Other more semi-quantitative scorings of mastings across the rest of the time series suggest a similar range in reproductive output.

Flowering is a precondition to fruiting, but the dependence is not exact. Heavy flowering was recorded in 1992, a mast year; but in 1991 there was also especially heavy flowering but no mast fruiting (Chuyong 1994, Newbery et al. 1998). In 1990 there was some low fruiting (flowering unmonitored), this coming though in the year after a main mast fruiting in 1989: further, 1993 had very little flowering and consequently almost no fruiting, and 1994 relatively high flowering but only scattered individuals fruiting Green and Newbery 2001a, 2002). From the later, more detailed, phenology recordings, 1995, 1997, 1998 and 2000 had strong flowering and were masting years, whilst 1996 and 1999 flowering was practically absent and had no masting (Newbery et al 2006a: Fig. 5). Whilst valvate bracteoles protect flower buds before anthesis, it is possible that the intense occasional shower could damage flowers enough to
interfere with pollination. This is the surmise for 1991, two years after the 1989 masting: fruiting was probably checked and masting was delayed to 1992. In 2004, the dry season started 43 days after 1 December 2003, on 12 January 2004 (Newbery et al. 2006a: Fig. 6): recall that the dry season for a given year starts in December the year prior. Flowering peaked over the week before and after that date. But in 2012, the season started 21 days in, on 22 December 2011, which was 1 month before flowering started in 2012, and ended another month later. (In both 2004 and 2012 there were no heavy showers that could have disturbed pollination in the first halves of those dry seasons.) These facets indicate that, firstly, occasional external and unpredictable influences can alter the processes behind a masting cycle; and secondly, the timing of flowering (also linked to the timing of leaf-exchange) can change by up to a month with respect to the start of the dry season. If internal tree nutrient levels do, via deterministic physiological mechanisms, trigger the flowering—which leads most often to fruiting at some level of strength (Newbery et al. 2006a), masting remains also subject to any climatic stochasticity causing interference to pollination (may be once in 10-15 years) and variability in dry season timing and intensity (every year).

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

Analysis of the seed and pod nutrient concentrations and amounts in relation to those in mature leaves indicated ratios of between ~ 0.1 and 0.2 for N, P, Mg and Ca, but substantially higher at 0.6 for K. This difference is very largely due to the low concentrations of the first four elements, and a much higher one for K in the pods. Pods were collected recently fallen. Caesalpods are hard and rather water-repellent for several weeks, so it is very unlikely they adsorbed much K coming down in canopy throughfall, or were they leached to any extent. Had that been a cause of an increase, then Mg should have increased too, yet it did not. Presently it is difficult though to explain why so much K was being invested in pods. The comparative leaf K values, coming admittedly from a retranslocation study where replication of bulked samples per date was small, do closely match those of mature leaves of plantation-grown *M. bisulcata* trees (averaging ~ 5.8 mg g\(^{-1}\); at ages of 13 to 18 years; D. M. Newbery unpubl. data). Whilst ECMs are strongly linked to P acquisition and uptake in the P-poor soils, K is also very low in availability at Korup (Gartlan et al. 1986), and the surface-soil root mat (with dense mycorrhizal networks) is an efficient collector of K (and Mg) coming down in throughfall (G. A. Neba, D. M. Newbery and G. B. Chuyong, unpubl. data). In plots at the same site, Chuyong (1994) found N, P, K, Mg and Ca concentrations of 13.8, 2.09, 6.41, 2.22 and 3.50 mg g\(^{-1}\) respectively in Mb seeds that fell in 1992. Pods were not separated in the 1992 general collections but ‘all reproductive parts’ in the HEM plots, those with high abundance of *M. bisulcata* had a mean K concentration of 6.04 mg g\(^{-1}\). Although other elements in fruits were albeit a little higher than for *M. bisulcata* alone in 1998, the earlier data well confirm the K values of interest. Investing P in seeds would presumably be important to the survival of establishing seedlings up until they could become infected with ECMs and link into the mycelial network. Could it be that also K, not P
alone—as for some time thought (Newbery et al. 1988, 2002), is a second key controlling
element of masting in the Korup groves, or as several indications suggest P and K might act
synergistically?

The main pattern explaining the masting time series was the sequence of relatively wet
dry season followed by relatively dry one. There was no evidence of water limitation to large
trees in the dry seasons because of their ability to root deeply, so this points to a soil or nutrient
factor governed by soil moisture content, in the upper soil layer where fine roots and ECMs,
form a root-mat, are most abundant and active in nutrient cycling. What is it about relative
dryness and wetness of the dry months that leads to these relationships? Possibly dryness
affected the fine roots and ECMs. The drier the dry season, then likely the more restricted the
root activity under limiting surface soil water conditions; which would possibly signal stored P in
the ECMs to be moved to intermediate 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 ‘m’ events occur in double-years
and twice later, mirroring the two ‘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. 4) 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 treelet 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).

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

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

Related considerations concerning carbon

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

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

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

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

*Rainfall and nutrient uptake*

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

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

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

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

The analysis of mast fruiting in 1989-2004 (Newbery et al. 2006a) used 150 trees across the whole P-plot, but the later recording 2009-2014 used a subset of 61 trees in the eastern half,
an area 100-500 N by 1000-1200 E, on the higher ground with denser stands and larger trees.

The masting time series could potentially have been confounded then by sampling extent changing over time, because for the earlier half (1989-2004) it was found that masting was significantly stronger on the relatively higher and drier sites of this eastern part of the P-plot compared with the rest of the plot (Newbery et al. 2006a). Allaying these doubts, the full and strong mastings in the second half (2007 and 2010) were confirmed by seed trapping across the entire plot (Norghauer and Newbery 2015). The two double-years, in the second half of the time series, were only moderate mastings despite being at the more favorable topographic location.

The very strong mastings achieved by *Dicymbe corymbosa* in Guyana are associated with pronounced ENSO peaks in radiation (Henkel et al. 2005, Henkel and Mayor 2019). However, this ectomycorrhizal caesalp, although phylogenetically very close to *M. bisulcata*, is unusual in that it reproduces annually also by sprouting, which must impose a considerable demand on C and nutrients for growth. For this reason, it might be conjectured that C stores are probably being continually used up and hence, to achieve a mast fruiting, a dependence on an additional boost in incoming radiation in those ENSO years would be necessary. Again, 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 ‘m’ double years. The evidence of an herbivore effect is strongest for fruiting in 2013-14 because of the detailed phenology data in 2011-12. It is tempting to suggest that something similar might have been happening in 2015 before the very similar masting pattern of 2016-17: alas, herbivore and tree phenology records were not possible during those later 3 years. A further unknown aspect is how herbivory may have induced stress hormones in the trees which, interacting perhaps with K levels, affected cytokinin concentrations.

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

**Refined updated hypothesis for mast fruiting in caesalps**

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

An interesting aspect is the feedback control that might operate by way of C going either into fine roots and ECMs, which would enhance nutrient uptake, or into wood storage (stem, branch and large root), which could sustain a next fruiting. The 2- or 3-year cycle is simply a consequence of the contingent conditions of these trees growing in low P soils aided by ECMs. Rainfall and radiation are stochastic processes, to some extent inversely related, which overlies the intrinsic deterministic cycle: the important difference between them is that rain, acting primarily on the soil, facilitates P release, acquisition and uptake (needed to accumulate P), and whilst C is needed also for fruiting, it is essential for root production and ECM maintenance that
makes this P uptake possible. That root growth should always precede fruiting in a masting year, the first in late-dry into early wet season (March-April), the latter in late wet season (September-October) decides the sequence unambiguously: C in the dry season will go to the root sink first and what remains stored, used for stem growth or reserved for fruiting when it happens. The low P supply is therefore the main determinant: C must be sufficient but does not appear to be decisive for the interval length. N and K will also be involved but the evidence more strongly supports the P thesis. Nitrogen is not limiting at Korup with ample N-fixation and aerial input (Newbery et al. 1997), and whilst K follows P in being intrinsically quite low in supply in Korup soils, the root-mat appears to be highly adapted to catching and retaining canopy-leached K and so enabling its efficient recycling (G. A. Neba, D. M. Newbery and G. B. Chuyong, unpubl. data). The K allocated to pods could like N be accommodated by wood ray storage.

Carbon and N will be important for masting, even when P and K are limiting and are the key storage resources, because all elements will be needed in their stoichiometric ratios in order to fill pods with seeds. As in other plant physiological problems, isolating reductionist approaches will not recognize the integrated nature of growth and reproduction. Carbon (sugars) and K are required for transport and storage, P will be bound into C-H-O structures which act as ‘carriers’. It is possible though that a small increase in C from radiation might have a non-linearly disproportional benefit to P transport and storage. Understanding masting physiology requires an integrated and dynamic approach, one of shifting sink strengths over time. After a last masting, roots would act as the strongest sink, then the stems (and rays and bark) and branches—part growth, part storage, and finally reproductive parts. No abrupt switches in C, in contrast with a threshold switch for P, but gradual altering of the components over a 2-3-year cycle. For this to operate it is necessary to hypothesize a feedback from the C-depleted branches...
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 seen 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 predominantly *ex hypothesis* 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 high flowering per crown then there
would be a deficit of C to fill pods, or pod production would decrease, or another cost incurred
(e.g. at the roots or wood production). But the evidence was that in *M. bisulcata* the relative
crown-cover with pods remained constant with size and, by broad inference, age. As a tree grew
to have a larger root system with ECMs to maintain, to acquire P and retain K, so when absolute
pod and seed output rose then the demand for P and K would also. As with C and N, we can expect that P and K is stored in ‘quick-release’ forms in wood and back rays of the stem and the main branches. A phenomenon often remarked is of one part of a large crown flowering and fruiting more than the others, which could be explained by a correspondingly more active root system of the tree, and a matching storage of nutrients in the wood and branches, on that side. (See Newbery et al. 2009 for the strong crown asymmetry in M. bisulcata.)

The arguments going from the nutrient concentrations in fallen litter through to the possibly the trees building up and storing P and K before masting are tenuous because of the many uncertainties about the processes involved. If some translocation occurs out of leaves before they are shed, then why are the P levels so high just before masting? If P was being actively stored for fruiting, it might be expected that it would be lower in concentration in the fallen leaves. However, the high concentration reflects that all the trees were well stocked with P by that time, the stores were full, or even over-full, and there was still plenty of P to fall. From earlier work, it was established that ectomycorrhizal species, especially M. bisulcata, drop P-richer leaf litter than non-ectomycorrhizal ones (Newbery et al. 1997) partly because the retranslocation was less (Chuyong et al. 2000), and it was argued that this allows the decomposition process to operate without P limitation, the 'fast forward' strategy. However, the concentration of K (to a lesser extent that of Mg also) reached a peak mid-interval and then fell just before masting. This could mean that K was being translocated into storage before fruiting. In general, the export of K and Mg from leaves of trees is usually low compared with that of N and P. Understanding the differences in dynamics of P and K in this context is highly challenging, and also explains why N showed no clear mast-interval trends. Whilst K was likely building up on soil colloids in wetter dry seasons, mineralized from fallen leaf, dead root and
old-pod during decomposition, and this process was more limited in the drier dry seasons,
suggest that K must also have been transported and actively stored in the tree between the prior
and mast years. To recycle more K via litterfall would involve a potentially high loss due to
leaching when the cation exchange capacity of the soil has already been reached, compared with
the seemingly tighter and ‘safer’ direct access by ECMs to organic P. This reliability aspect
might then favour P over K as the better controlling factor in masting.

Phosphorus storage and control

What could the likely form of storage of P in trees be? Since Bieleski (1973) the most
likely candidate is inositol hexakis phosphate (= phytic acid; C₆H₁₈O₂₄P₆). It has been shown
many times to be the main storage form in seeds, and has been detected in stem and roots. It
forms salts with Ca, K, Mg, Mn and Zn, and in soils occurs commonly bound to Fe. It occurs in
19 hexa-structures which are interconvertible (Raboy 2003). It is viewed as the most frequent P-
storage form when P is in excess, that is in passive storage; the P is readily retrievable and
mobilizable. Other molecules can have seven or eight atoms of P but seem less common (Raboy
2003). Inositol hexakis phosphate is involved in cell metabolism, in ATP regeneration, RNA
export and the repair of DNA. It is prominent in cell storage biochemistry, which may make it a
candidate for active storage. However, so very little has been researched in this area, and
accounts for trees are very sparse. A notable exception is the study of Kurita et al. (2017),
showing P storage in *Populus alba*, followed by release in spring, and indicating perhaps a
common function in many deciduous tree species. It is conceivable that the same mechanism
could operate in seasonal tropical trees and even be a basis to P storage for mast fruiting species.
How inositol hexakis phosphate is linked to polyphosphate formation in roots and mycorrhizas,
and comes under hormonal control remains unclear.
In an experiment with *Eucalyptus grandis* seedlings, comparing low and high P media, Mulligan (1988) detected stored P in the form of esters and residual P (mostly phosphorus proteins), especially in roots, and more so the low P medium. The idea is that these stores buffer the plant (maybe actively stored), from there P can be mobilized and sent to other stores in the shoots. In a similar vein, Netzer et al. (2017) comparing mature *Fagus sylvatica* stands, one on high and one on very-low P available soils, found that in the latter P built up in roots in late summer, and from there was moved on to stem and branches, suggestive of at least two storage sites in a series enabling adaptation to the poor site. However, hardly anything is known about how P stores are internally controlled, or how hormones signal transfers of P (Rennenberg and Herschbach 2013), which could give even a lead as how P might be built up in stores in masting intervals, and once a threshold level is met how the switch to flowering is signaled.

Much evidence points to senescence in leaves, and possibly also pod formation, involving cytokinins too (Marschner 2012). Chiou and Lin (2011) have proposed different hypothetical models for inorganic P being regulated by cytokinins and sugar levels. How these promising models can be extended to storage and release of P has yet to be worked out. The strongest candidate for the elusive ‘florigen’ is a now widely held to be a flowering locus T [FT-] protein, which again appears to be controlled by a cytokinin (Turnbull 2011). Cytokinins act at long distances and are bidirectional in their effects, both of which might hypothetically implicate them in inositol hexakis phosphate metabolism and P storage. It remains likely that floral initiation in *M. bisulcata* takes place at the end of the wet season, before leaf exchange occurs in the dry season (see discussion in Newbery et al. 2006a). Earlier results on apple (*Malus*) trees suggested already that a two-way process of hormonal control could be operating (Davis 1957), and the idea that sugars and other NSCs destined for the usually stronger root sink (Goldschmidt and
Golomb 1982, for mandarin (*Citrus*), and Hansen et al. 1982, for prune (*Prunus*)—on K-deficient soils) might be diverted to the flowering meristem sinks under the control of gibberellins (Sachs 1977). How exactly the ‘switch’ occurs remains obstinately elusive (Monselise and Goldschmidt 1982, and to the present day). The precise consistency of alternate bearing in *Pistacea* orchards has been questioned on statistical grounds (Rosenstock et al. 2010).

**Active storage hypothesis**

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

**Nutrients in alternate bearing of tree crops**

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

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

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

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

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

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

**Role of environmental stochasticity**

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

The systems view would postulate a feedback control to avoid such chaos but it could allow for an unpredictable mix of 1-, 2- and 3-year cycles over time to the same effect in thwarting predator tracking. For a limited resource like P, such a system means regulation of internal fluctuations across the tree parts within a masting cycle, so that some equilibrium in the
P dynamics is maintained medium-term. An economy of scale which itself involves a mechanism for P distribution would facilitate masting when based on storage and thresholds of that same resource. In this respect, ectomycorrhizal networks, which enable P acquisition and uptake (and possibly P storage), could bring about an equilibration of P across the connected roots of neighbouring trees, which would allow a contemporaneous storing and triggering of mast fruiting, as P levels rose in concert across all trees in the population. In the case of *M. bisulcata* in this study, the key climate variables vary in a somewhat normal way, and it is unlikely they can cue masting in a simple directly-linear manner. However, if wetter dry seasons lead to non-linear increases, or pulses, of P-and/or K-uptake, coordinated across the forest, synchrony is also possible. The network idea would also explain why one or both *Tetraberlinia* species often mast fruit along with *M. bisulcata*, because they largely share the same mycorrhizal species (Newbery et al. 1988, 2000). The non-stationary aspect of the main hypothesis suggests a finely-tuned evolved ecophysiological system in *M. bisulcata* allowing it to respond to variation of the climate in order to maximize its fitness.

**Conclusions**

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

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

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

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Author Contributions

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

Conflict of Interest  None.

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

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

*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).

<table>
<thead>
<tr>
<th>l-mast (n)</th>
<th>year</th>
<th>N</th>
<th>P</th>
<th>Ca</th>
<th>K</th>
<th>Mg</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 (30)</td>
<td>2011</td>
<td>16.06 ± 0.25</td>
<td>0.597 ± 0.018</td>
<td>14.71 ± 0.58</td>
<td>4.41 ± 0.11</td>
<td>3.40 ± 0.13</td>
</tr>
<tr>
<td>1 (20)</td>
<td>2002&lt;sup&gt;a&lt;/sup&gt;</td>
<td>17.39 ± 0.33</td>
<td>0.632 ± 0.026</td>
<td>NA</td>
<td>5.58 ± 0.45</td>
<td>3.43 ± 0.17</td>
</tr>
<tr>
<td>2 (5)</td>
<td>1991&lt;sup&gt;b&lt;/sup&gt;</td>
<td>15.72 ± 0.66</td>
<td>0.692 ± 0.025</td>
<td>13.99 ± 0.82</td>
<td>4.67 ± 0.23</td>
<td>3.89 ± 0.17</td>
</tr>
<tr>
<td>3 (5)</td>
<td>1992&lt;sup&gt;b&lt;/sup&gt;</td>
<td>19.33 ± 0.55</td>
<td>0.809 ± 0.047</td>
<td>12.70 ± 0.90</td>
<td>2.44 ± 0.07</td>
<td>2.53 ± 0.09</td>
</tr>
<tr>
<td>&lt; 1 (6)</td>
<td>1998</td>
<td>18.27 ± 0.64</td>
<td>0.836 ± 0.057</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>

<sup>a</sup> Schwan (2003); <sup>b</sup> 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.

<table>
<thead>
<tr>
<th>Element</th>
<th>Concentration (mg g⁻¹)</th>
<th>Amount (kg ha⁻¹ yr⁻¹)</th>
<th>Ratio [fruit: leaf]</th>
<th>Reproductive allocation (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Seed</td>
<td>Pod</td>
<td>Leaf⁵</td>
<td>Seed</td>
</tr>
<tr>
<td>N</td>
<td>14.5</td>
<td>3.80</td>
<td>22.3</td>
<td>0.770</td>
</tr>
<tr>
<td>P</td>
<td>1.80</td>
<td>0.24</td>
<td>1.18</td>
<td>0.096</td>
</tr>
<tr>
<td>K</td>
<td>7.40</td>
<td>6.13</td>
<td>5.91</td>
<td>0.393</td>
</tr>
<tr>
<td>Mg</td>
<td>3.01</td>
<td>1.17</td>
<td>3.77</td>
<td>0.160</td>
</tr>
<tr>
<td>Ca</td>
<td>3.77</td>
<td>2.17</td>
<td>13.2</td>
<td>0.200</td>
</tr>
</tbody>
</table>

⁵ as reported in Green & Newbery (2002; Table 1); mature, green leaves, from Chuyong *et al.* (2000; Table 6); 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; RA = fruit density/(fruit + leaf densities).
Legends

Fig. 1. The time series of mast fruiting of *Microberlinia bisulcata* at Korup, 1989-2017. 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.

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·10^{-3}); and (f) the difference in radiation (*radiation*) between successive years (current minus prior). Symbol colours: brown, full; orange, partial; and green, no; masting event.

Fig. 3. 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 (a) the current, and (b) prior, year’s dry season. Symbol colours: brown, full; orange, partial; and green, no; masting event recorded.

Fig. 4. 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).

Fig. 5. Changes in the mean scores of five phenological stages of *M. bisulcata* trees at Korup in (a) 2009-2010 and (b) 2011-2012. Stages: leaf fall (blue), leaf flush (purple), flowering (green); immature (yellow) and mature (red) pods. The horizontal red lines indicate the span of the dry season for each year (see also Appendix 5: Fig. S2).
Fig. 1

The graph shows the masting intensity over the years from 1989 to 2016. The intensity peaks regularly with some fluctuations in certain years. The years 1998, 2004, 2007, and 2013 are marked with "C" indicating significant events or changes in masting intensity.
Fig. 3

(a) In(rain)

(b) In(rain.1)
Dec.09 Jan.10 Feb.10 Mar.10 Apr.10 May.10 Jun.10 Jul.10 Aug.10 Sep.10

Date

(a) 2009–2010

Score

(b) 2011–2012

Stage

br–pods
fall
flower
flush
gr–pods

Fig. 5

Stage

br–pods
fall
flower
flush
gr–pods

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