PHILOSOPHICAL TRANSACTIONS B

Introduction

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The ecology and evolution of synchronized reproduction in long-lived plants

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Populations of many long-lived plants exhibit spatially synchronized seed production that varies extensively over time, so that seed production in some years is much higher than on average, while in others, it is much lower or absent. This phenomenon termed *masting* or *mast seeding* has important consequences for plant reproductive success, ecosystem dynamics and plant–human interactions. Inspired by recent advances in the field, this special issue presents a series of articles that advance the current understanding of the ecology and evolution of masting. To provide a broad overview, we reflect on the state-of-the-art of masting research in terms of underlying proximate mechanisms, ontogeny, adaptations, phylogeny and applications to conservation. While the mechanistic drivers and fitness consequences of masting have received most attention, the evolutionary history, ontogenetic trajectory and applications to plant–human interactions are poorly understood. With increased availability of long-term datasets across broader geographical and taxonomic scales, as well as advances in molecular approaches, we expect that many mysteries of masting will be solved soon. The increased understanding of this global phenomenon will provide the foundation for predictive modelling of seed crops, which will improve our ability to manage forests and agricultural fruit and nut crops in the Anthropocene.

This article is part of the theme issue 'The ecology and evolution of synchronized seed production in plants'.

1. Introduction

Why are there so many flowers, fruits or seeds on most plants of the same species in some years and not in others? This age-old question is surprisingly difficult to answer. Interannual cycles have always played a central role in human interactions with the environment. The relationship between weather and resource dynamics, such as crop fluctuations and plant regeneration, likely constituted some of the earliest ecological knowledge passed over generations, particularly before such dynamics were stabilized with the onset of agriculture [1]. For humans, the importance of extensive temporal variation and spatial synchrony in seed production within and across plant populations—a phenomenon broadly termed *masting* or *mast seeding*—has transitioned from a matter of survival, starvation or migration to one of arboriculture, forestry, wildlife management, conservation and disease prevention [2–5].

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Table 1. Five questions about the ecology and evolution of mast seeding and relevant contributions in this theme issue.

	level	question	references
1	proximate	what are the mechanisms that drive seed production and its synchrony?	[2,7,35–43]
2	ontogeny	how do the variability and synchrony of seed production change throughout individual and population development?	[35,39]
3	adaptation	what are the fitness costs and benefits of masting?	[37,40,41,43–45]
4	phylogeny	how (often) and why did masting evolve?	[42,45]
5	application	what is the role of masting in plant–human interactions?	[2,5,7,40]

The questions of how and why many plant populations produce 'boom and bust' seed crops, which can be synchronized over large areas, have piqued the interest of generations of ecologists concerned both with applications of masting and with developing a mechanistic understanding of this 'mysterious' phenomenon [6]. Progress in the field of masting has often moved as slowly as the lives of the long-lived plants that we study [7]; for example, simply capturing the key properties of masting requires years of observations of seed crops over many individual plants [8]. Several reviews have guided the study of masting over the past three decades and encouraged researchers to make these observations. These syntheses have developed working definitions of mast seeding [9], explored the taxonomic and functional breadth of plants that mast [10,11], quantified the large geographical scale at which masting can occur [12], explored the role of plant physiological resource dynamics in masting [13], distinguished the proximate mechanisms and ultimate (evolutionary) consequences of masting [14] and highlighted the need for new lines of experimental inquiry into masting [3]. Thanks to millions of observations of seed production, numerous studies asking questions about the causes and consequences of masting, and syntheses that put these pieces together, we now have plausible answers to many of the mysteries of masting (*sensu* Koenig & Knops [6]) articulated in previous decades.

Several recent advances in the study of masting provided the impetus for this special issue. These include a renewed focus on the adaptive consequences and evolution of masting, crucial interactions with disturbances and work addressing the response of masting to climate change. Furthermore, the amount and extent of available data have increased, resulting in several global perspectives [15,16], elucidating the emerging roles of teleconnections and climate change [17] and shedding light on the selection pressures for masting [18,19]. Finally, a publicly accessible global database of plant reproductive time series, MASTREE+, was recently assembled by a team that includes the editors of this theme issue [20]. Inspired by the diverse data sources, we reached out to a broad international group of colleagues to solicit contributions that broaden the geographical, taxonomic and thematic scope of masting research.

Due to unforeseen developments, including the effects of the COVID-19 pandemic, the special issue ended with less geographical representation, thematic breadth and diversity in authorship than envisioned. It thus continues a long tradition of masting research focused on temperate forests in Europe, North America, Japan and New Zealand, biases that exist more generally across ecology [7,21,22]. In masting ecology, this is in part a reflection of the underlying biogeography

of masting [16], but it clearly neglects important masting-dominated systems in other boreal and temperate systems [23,24], and the emerging evidence that masting is also an important reproductive strategy in the tropics and arid systems [25–27]. As evidenced by the pioneering work on the adaptive value and proximate mechanisms of masting in tropical *Shorea* species [28,29], major insights can be gained from studying these systems. Furthermore, given the value of non-timber forest products that depend on masting, the cascading effects of masting on ecosystem processes and the role of masting as a potential driver of zoonotic disease dynamics, there is an urgent need to expand the geographical scope of masting research beyond relatively well-studied regions [30–33]. Therefore, this special issue is only a first step towards a more inclusive, as well as geographically and taxonomically representative field of masting research. We hope that the articles in this issue inspire scientists and students from around the world, particularly from related fields such as physiology, climatology or molecular biology, to pursue questions related to the variation and synchrony of seed production in plant populations in space and time.

To provide a broad overview of the field and the contributions of this special issue, we reflect on the current understanding of masting along four questions inspired by the framework by Tinbergen [34], while including a fifth question of the role of masting in plant–human interactions (table 1). For each question, we describe the general state of the science, discuss how recent work, including from this issue, has changed our understanding of masting, and sketch out promising avenues of research.

(a) Proximate mechanisms

Masting emerges by combining individual annual variability in seed production and spatial synchronization among individuals [13,14]. Resource dynamics, environmental variation, genetic and hormonal regulation, pollen limitation and their alignment through space and time are factors that generate variability and synchrony [3]. The specific way each of these proximate factors drives masting is highly variable among plant species and even populations [46], providing an exciting avenue for research but also creating a challenge in predicting the responses of masting to climate change [35]. For example, LaMontagne *et al.* [36] found that in North America conifers, masting is cued by the difference between summer temperatures 2 and 3 years before seed fall, supporting the so-called ΔT model (i.e. $\Delta T = T_3 - T_2$). If climate change affects mean temperatures more than their interannual variability, masting would be predicted to be relatively robust to climate change

under the ΔT model [47]. In support, conifer masting in North America remained stable over 40+ years despite increasing temperatures [36]. By contrast, when masting is driven by seasonal weather anomalies, the frequency of cues will change under warming, which can affect the interannual variability and synchrony of seed production [44,48]. Thus, multiple cueing mechanisms exist that will generate very different plant responses to climate change and may result in community shifts if reproductive strategies of some plants are better suited to withstand warming (conifers [36]) than others (beech and oaks [49,50]). Such differences are further complicated by the way climate change is affecting large-scale modes of climate variability with uncertain consequences for the spatio-temporal alignment of proximate cues of masting in several regions [37], along with different climate sensitivities among species [38]. Moreover, in some species, interactions with disturbances such as fire, drought, flooding or windthrows drive the extent and synchrony of seed production, as found in fire-adapted scrub oaks in Florida, USA [39]. The effects of climate change on masting will, therefore, be additionally complicated by the rate of change in the relevant disturbance regime [40].

Experiments identifying the proximate mechanisms of interest and the response of those mechanisms to stress caused by global climate change are essential for progress in this field [3,51–53]. Other useful approaches examine processes using mechanistic models and increasingly available large datasets [20]. By combining observations and ecophysiological-based models, researchers are starting to untangle the dynamics of resource allocation [54] and highlight unexploited potential of process-based models of masting in larger vegetation modelling efforts [55].

A framework of testable hypotheses is particularly useful to guide such efforts. For example, if a certain process is an important driver of masting in a species, how do we expect masting to change under increasing environmental stress? The expected insensitivity of the ΔT mechanism to changing weather anomalies is one example, but examination of plant responses to other hypothesized mechanisms is also possible using the temporal depth and taxonomic diversity of large datasets. Other pressing questions may also be answered with interspecific comparisons. For example, how do proximate drivers change across species that have differing levels of variability and synchrony? How do some species generate very high synchrony over large areas while others do not?

Finally, few studies to date have used a wide range of tools in functional genetics to better identify the physiological processes and pathways involved in masting [41,42]. Techniques such as associational mapping and quantitative trait locus analysis provide tools to better understand genetic variation in the masting process [41,56]. By deciphering the molecular processes that integrate the various factors associated with large or small annual seed crops, it may not only be possible to understand masting but also to alter patterns of seed production through breeding or hormonal cues.

(b) Ontogeny

As a spatio-temporal, population-level phenomenon, masting emerges from the synchronization of individual-level behaviour of plants over large geographical areas [8]. Investigating differences among individuals, as well as changes within individuals over time, therefore builds a foundation for understanding the mechanisms and selective costs and benefits of synchronized reproduction [10]. Aside from the commonly observed pattern of extensive growth investment before first reproduction, the onset and development of seed production as a function of size (or age) of most perennial plants is poorly understood [57,58]. It is unclear how the extent, variability and temporal autocorrelation of seed production scale with individual age or size, how these relationships change as a function of the demographic structure of populations, or how reproductive synchrony emerges over time. For example, do complex long-term patterns of synchrony emerge from simple mathematical rules underlying individual behaviour, as has been hypothesized for bamboo flowering patterns [59]? What are the trade-offs of flowering and seeding earlier or later in life? An ontogenetic perspective is central to understanding life-history trade-offs, particularly between reproduction, growth and defences [60], linking the proximate and ultimate drivers of mast seeding. More generally, the ability to predict mast seeding depends on the understanding of individual tree behaviour, both on an ontogenetic trajectory and in response to abiotic and biotic environments.

Progress has been made in understanding the ontogenetic development of fecundity [61,62], but the effect of tree age and size on masting behaviour has often been neglected. Comparisons among age or size groups have provided important initial insights. For example, Bogdziewicz *et al.* [63] found that interannual variability in seed production decreased with plant size and stabilized above a fecundity threshold. Minor & Kobe [64] found that seed production in Northern hardwood forests in North America was dominated by a few large 'super-producers' that showed lower temporal variability and higher synchrony than the overall population. Similarly, when comparing individual valley oaks (*Quercus lobata*), Pesendorfer *et al.* [65] found that large trees with high fecundity exhibited lower variability and more negative temporal autocorrelation than smaller trees. Combined, these findings illustrate that the variability and autocorrelation of seed production change over an individual's lifetime. However, even in the longest available time-series data for individual trees, only a fraction of the potential lifespan is covered, thus leaving questions about the interactions between ontogenetic processes and environmental conditions, and the possibility of changes in synchrony with neighbouring trees.

Ontogenetic studies of masting also have implications for the demographics of future plant communities and ecosystems. For example, in forests where masting is a key process determining plant recruitment, age- and size-related changes in masting will have implications for climate change resilience, with wider cascading effects on the structure and dynamics of food webs [66]. Evidence of age-driven changes in masting was recently reported for Polish forests, where increasing stand age was the main driver of long-term increases in interannual variability of seed production, while climate change had negligible effects on masting behaviour [67]. Direct links between such changes in masting, plant recruitment and broader trophic effects have not yet been reported, but numerous modelling studies indicate the potentially dramatic consequences of such shifts in masting behaviour (e.g. [68,69]). In newly established forests, or those recovering from disturbance, ontogenetic changes in masting will have important implications for management [5], irrespective of any parallel changes in masting resulting from environmental change [35].

As individuals reach the end of their lifespan, the question of declining fecundity or terminal investment—increased reproductive effort before death—arises. Life-history theory predicts that as mortality increases with senescence, resources should be allocated to reproduction rather than growth or defences [70]. This phenomenon is commonly found in iteroparous animals [71], but 'folk knowledge' about similar effects on plant reproduction drives a persistent misconception. While certain stressors drive trees to temporarily increase reproduction, there is no evidence that impending natural death is associated with bumper crops. In fact, seed production appears to stagnate or decline before death [61,72,73]. Interestingly, evidence is accumulating that long-lived trees experience 'negative senescence' during which mortality rates decline with age after surpassing a threshold [74]. More broadly, the growth and reproduction of old and ageing trees are important aspects of the ongoing discussion about forest management under rapidly accelerating climate change [34].

Looking ahead, the study of individual development will help our understanding of the contribution of genetic and environmental effects to the reproductive phenotype, clarify the role of demographic composition and facilitate conservation planning. Long-term cohort studies, provenance plots and quantitative genetic approaches will provide critical insights into the fitness consequences of masting.

(c) Adaptation

What are the fitness benefits of variable and synchronous reproduction? Research on the evolutionary ecology of masting has largely focused on hypotheses pertaining to economies of scale (EoS), where density-dependent mechanisms during flowering, pollination, fruiting and seeding increase reproductive efficiency and individual fitness [9,14,75,76]. Pollen limitation, which can hamper seed production, varies between years as a function of weather conditions or flowering synchrony [51,76–78]. While effective fertilization is strongly influenced by pollen availability, it is still unclear what advantage is provided by interannual variation in comparison to continued flowering at stable levels, though the answer may lie in the benefit accruing to low-density populations through mass flowering [76].

Interactions with animals during fructification, seed abscission and dispersal vary with population-level seed production levels in current and previous years. Predator satiation—the reduced *per capita* rate of pre- and post-dispersal seed predation in years of large seed crops—is commonly found for seeds infested by insects while on the plant or depredated by vertebrates once on the ground [11]. However, there is also evidence that predator satiation effects may not apply universally, particularly in old-growth forest stands with slow recruitment [79]. The animal dispersal hypothesis, which posits that animal-mediated seed dispersal benefits increase with seed production levels, has received mixed support, likely because seed fate effects depend on many factors including disperser life history and mobility [80,81]. Zwolak *et al.* [43] use simulation modelling to show that the effects of masting on the population dynamics and caching behaviour of scatter-hoarders are mutually dependent. By decreasing the degree of pilfering, the satiation–starvation cycle induced by seed masting promotes the evolution and maintenance of seed caching behaviour.

In the sequential steps of the reproductive cycle, multiple EoS mechanisms can interact, so that changes in flowering behaviour can result in reduced predator satiation. In European beech (*Fagus sylvatica* L.) trees, for example, increasing temperatures have reduced the sensitivity of individual trees to the masting cues, resulting in more asynchronous flowering and seeding [44]. Asynchronous trees that show reduced variability in seed production consequently experienced higher levels of pre-dispersal seed predation [82], highlighting that EoS-related fitness consequences can result in selection for mast seeding at the individual tree level.

Among evolutionary hypotheses overlooked in the past, the environmental prediction hypothesis is receiving new support thanks to increased data availability and resulting insights into spatio-temporal patterns of masting [83,84]. This hypothesis proposes that plant populations synchronize their mast years based on weather cues that also predict favourable conditions for germination, seedling emergence and survival. Considering how natural disturbances can favour subsequent plant reproduction provides a new perspective on this process. This includes beneficial changes in light regime, soil conditions, water and nutrient availability for offspring. Vacchiano *et al.* [40] highlight how drought, heat waves and wildfires are foreshadowed by weather conditions that can also act as proximate cues of masting. Evidence suggests that changes in disturbance regimes promote eco-evolutionary feedbacks selecting for masting behaviour [83,84].

Large-scale modes of climate variability, such as El Niño–Southern Oscillation (ENSO), have been shown to align spatio-temporal patterns of both masting and disturbances, thus increasing the probability of seed dispersal in a disturbed environment that is favourable for seed germination and seedling establishment [83,84]. Such climate modes influence reproduction and recruitment both directly via weather patterns that align proximate mechanisms of masting through time and space, and indirectly by promoting the emergence of density-dependent EoS over large areas, and by synchronizing lagged but in-phase ecosystem dynamics conducive to survival of offspring [38]. Of course, apparent cases of environmental prediction and EoS may occur at the same time and are not mutually exclusive [9,14]. Ascoli *et al.* [37] suggest the hypothesis that large-scale modes of climate variability have the potential to 'bridge' proximate and ultimate causes of masting, selecting for variable and synchronous reproduction. They also discuss the spatial scales at which reproduction synchrony is relevant to adaptive benefits for masting.

(d) Phylogeny

Phylogenetic analyses of masting provide potential answers to many important questions. How is masting as a trait distributed on the Tree of Life? What are the evolutionary history and potential functions of masting? Has it emerged recently, or is it ancient? Is it consistently associated with other plant traits, like wind pollination? Are there evolutionary consequences of masting associated with adaptive radiations, extinctions or other macroevolutionary events? Historically, a tendency towards masting in some taxonomic groups of plants, such as pines and oaks, has been noted. Phylogenetic comparative studies confirm this observation by demonstrating a phylogenetic signal (clustering on a phylogeny) of masting [16,18,45,85,86]. Nevertheless, there is still considerable variation

in masting even within closely related plant clades. For example, within oaks (genus *Quercus*), the interannual population-level coefficient of variation of mean seed production—a common measure of masting—varies roughly six-fold among species, and crop sizes of different species are associated with different weather cues [86]. Masting is common in some ancient plant clades, such as cycads, suggesting that mast seeding might be nearly as old as seeds themselves [87]. However, using observations of extant species to infer ancient history may be misleading, given evidence supporting a model in which masting can evolve relatively quickly [85]. To date, all our inference into the history of masting as a trait comes from phylogenetic comparisons of extant species, and it may be worthwhile to explore the degree to which masting can or cannot be inferred from the paleobotanical record.

There has been a long-running debate as to whether masting is an immediate, short-term response of plants to annual variations in weather, or if masting is an evolved strategy over a lifetime that enhances fitness via an EoS such as predator satiation, increased pollination efficiency or environmental prediction [11]. Phylogenetic associations between masting and other plant traits, such as wind pollination, and seed dispersal strategy have been one of the primary lines of evidence to argue that masting is more than a short-term response to environmental variation [10,11,16]. Nevertheless, other comparative studies suggest that our understanding of masting evolution is far from complete. For example, masting appears to emerge disproportionately in species that cope with nutrient imbalances in their tissues and that live in high-productivity habitats [18]. However, the direction of causality is unresolved and thus masting intensity could simply be amplified by nutrient scarcity [88]. Little is known about the broader macroevolutionary consequences of masting, but Dale *et al.* [45] provide important first steps in this direction. Their analysis indicates that the net effect of masting on macroevolutionary patterns appears to be minimal as it is not associated with altered rates of speciation.

Part of the problem in inferring phylogenetic patterns in mast seeding has been the lack of data, along with taxonomic and geographical biases in studies of seed production. As this problem is overcome, it is likely that our understanding of the evolution of masting seeding could drastically change. For example, in several parts of the world, synchronous, community-wide mass flowering and fruiting events in wild and domestic plants have been observed [2,38], while in other places, even closely related plant species produce seed crops on their own schedule [89]. These patterns remain a mystery, and one that may be addressed with future phylogenetic analyses.

(e) Applications

One major motivation to study masting is that it is an important ecosystem process that affects how we manage the environment [5]. A consideration of masting is important when assessing the future of the world's forests and other habitats dominated by masting species, monitoring and managing the populations of rare masting plants and seed-eating animals, as well as collecting and dispersing seed for restoration or assisted migration. The forest gap models, landscape models and ecosystem models widely used to simulate vegetation change and inform management rarely include realistic parametrization of seed production (i.e. masting). Nevertheless, studies indicate that extending models to

include masting increases realism and can, for example, substantially affect predicted vegetation responses to disturbance [3,55,69]. This indicates that future work to incorporate masting into such models will improve estimates of vegetation dynamics, and associated management decisions. The European Union's Biodiversity Strategy 2030 [90] calls for the planting of an additional 3 billion trees within a decade, an effort that will be strongly impacted by seed availability and its spatio-temporal variability. In the Anthropocene, the focus has also shifted to controlling invasive plants and animals, forecasting the risk of zoonotic diseases that cycle with mast crops, and collecting seeds for food [5], as masting also occurs in many cultivated fruit and nut crops. In agriculture, this phenomenon is usually known as 'alternate cropping' or 'alternate bearing' and is characteristic of many commonly grown fruit crops, including apples, cherries and chestnuts [2]. Furthermore, patterns present in wild masting species, such as higher interannual variation in wind-pollinated species compared to animal-pollinated, are also present in horticultural systems. This has diverse consequences for the global food supply and farmer livelihoods, as discussed in this issue by Garcia *et al.* [2]. Fundamentally, masting creates year-to-year variation that has important ecosystem consequences. Accounting for that variation when modelling community demographics, analysing plant response to climate change, and collecting seeds for restoration or assisted migration can greatly improve their success [5,55,91].

Mast crops are often somewhat predictable based on environmental conditions and previous crops, and this information can be used to improve the timing of management actions. In ecosystems that are influenced by disturbance such as wildfires, windstorms and silvicultural treatments, the timing of the next bumper seed year is crucial to the ability of plants to regenerate, and successful forecasting of mast years may determine the outcome of chosen restoration strategies [91]. However, this is extremely challenging to incorporate into restoration planning, as disturbance events often require immediate action from land managers. When possible, forest managers strive to time silvicultural interventions in relation to masting, to increase the number of dispersed seeds reaching the ground under improved light and soil conditions, or limit post-dispersal disturbance of seeds that would hamper natural regeneration dynamics [91,92].

The ecological applications of masting concepts extend beyond plants. Bumper seed crops in forest trees create pulses of food resources and cause population booms in primary consumers that can reverberate across trophic levels and thus affect the timing of management actions aimed at animal populations [93,94]. For example, forecasts of seed and fruit crops in New Zealand inform both the management of invasive mammals and translocation programmes of the endangered kākāpō [95,96]. Similarly, the effect of masting on zoonotic, tick-borne disease incidents in human populations, driven by the effect of cycling rodent populations on tick numbers, can be forecast with a time horizon of up to 2 years [97]. In other cases, where forecasts of seed and fruit crops are not made, interannual variation in seed crops is an obstacle to environmental management. For example, variation in seed crops is a major hurdle to local seed collection for human consumption [98] and restoration projects [89]. Developing and implementing widespread predictive forecasts of mast seed crops and failures are one way that the scientific study of masting could improve management actions and accurate predictions of the nexus between

vegetation ecology, climate change and natural resource management.

2. Conclusion and outlook

This issue aims to initiate a broader taxonomic, geographical and culturally diverse approach to masting research and applications. Several promising themes of future research are highlighted, including molecular deciphering of pathways underlying flower induction and seed production, the role of resource-related environmental processes at the individual level, expanded analyses based on global datasets, drivers of synchrony and the potential for forecasting seed production. Of the five facets of masting considered here, proximate mechanisms and adaptive value have been investigated most thoroughly and are thus best understood, while ontogeny, phylogeny and potential applications to plant–human interactions are still relatively poorly understood. With the emergence and increased value of ecological forecasting for interactions between humans and their environment, we anticipate that masting research and its many interfaces with other disciplines will continue to advance at a rapid pace.

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