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NOTE AND COMMENT

Gianluca Piovesan · Jonathan M. Adams

The evolutionary ecology of masting: does the environmental prediction hypothesis also have a role in mesic temperate forests?

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Abstract The evolutionary advantages of mast seeding in mesic temperate forests are reviewed with reference to the whole plant's lifecycle. The aim of this article is to give attention to the environmental prediction hypothesis as an evolutionary aspect of closed-forest dynamics that need to be tested in field studies and modelling. It is suggested that the year after a period of water stress (or other suboptimal conditions for growth) trees respond with high seed production. Due to an understory environment favorable for prolific establishment of seedlings (i.e., more light at the forest floor) this may give rise to a pulse of regeneration. Thus, understanding masting may require a multi-faceted approach including the study of the ecology of the trees themselves beyond pollination and seed predation, and including gap ecology and patch dynamics with special attention to patterns of forest regeneration.

Keywords Mast seeding · Evolutionary ecology · Forest dynamics · Synchronized reproduction · Drought

The evolutionary advantages of masting of forest trees are assumed to be associated with improved pollination and seed-predator satiation (e.g., Kelly and Sork 2002; Shibata et al. 2002; Koenig and Ashley 2003; Koenig et al. 2003; Iwasa and Satake 2004). Moreover scatter-hoarding rodents can select for both large seed crops and large seeds, which may reinforce mast seeding (e.g., Jansen et al. 2004). A storage-size-dependent strategy was also proposed to explain the conditions that generate mast reproduction (Yamauchi 1996). Other (post-seed dispersal) explanations for the evolutionary ecology of mast seeding in forest stands are generally viewed with scepticism.

The Forum paper on mast fruiting and ENSO cycles in the tropics has opened up a new discussion on the evolutionary advantages of mast seeding in forests (Williamson and Ickes 2002). Here, we suggest that the environmental prediction hypothesis (Kelly 1994) can be extended from tropical (Williamson and Ickes 2002) and boreal forests (Selås et al. 2002) to explain masting behavior in mesic temperate regions, particularly in beech (*Fagus* and *Nothofagus*). The aim of this note is to give attention to the environmental prediction hypothesis as an evolutionary aspect of closed-forest dynamics that need to be tested in field studies and modelling (i.e., coupled map models, Iwasa and Satake 2004).

It has long been noted that masting behavior in beech occurs 1 year after a massive floral induction, triggered by a warm, dry summer (Piovesan and Adams 2001). In Norway spruce, and other temperate and boreal trees, particularly high seed output also follows a warm, dry summer (e.g., Ogden 1985; Houle 1999; Selås et al. 2002; Greene and Johnson 2004, and references therein). The observational and experimental demonstration that drought has a stimulating effect on floral induction may explain, at least for the genus *Fagus*, which we have studied in detail (Piovesan and Adams 2001), some evolutionary aspects of this widely conserved pattern of reproductive behavior. The adaptive advantage of such massive reproductive behavior synchronized by drought (or warm summers, see Richardson et al. 2005) may be evident if one considers it on a longer time scale, from the point of view of the tree's ecology within a forest. The argument rests upon a series of observations and postulates regarding the mechanisms causing masting, selective forces, and economies of scale (Norton and Kelly 1988).

In mesic forests, asymmetric competition for light is an important driving force (Yoda et al. 1963; Weiner 1990). Trees in mesic forests, such as the shade-tolerant beech, must compete in dense stands, and resource allocation systems have also evolved under this selective

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G. Piovesan (✉)
Department of Technologies, Engineering,
Sciences of the Environment and Forests, University of Tuscia,
Via S. C. de Lellis, 01100 Viterbo, Italy
E-mail: piovesan@unitus.it

J. M. Adams
Biological Sciences Department, Rutgers University,
Newark, NJ 07102, USA

pressure (Sork 1993; Silvertown and Dodd 1999; Westoby et al. 2002). During the earliest phases of life (the seedling, sapling and pole stages) beech allocates all of its resources to vegetative growth, especially height increment, in order to survive competition and enter the canopy. In these stages of the forest cycle, the stands are too dense to permit seedling establishment. At a variable age (30–90 years), depending on the intensity of competition experienced and the fertility of the soil, the few trees that have survived self-thinning become reproductive according to a masting pattern.

The assumption that there are costs of reproduction remains an important aspect of life-history evolution, especially in explaining masting behavior. The biology of mature trees is characterized by shifting the allocation of resources between vegetative growth and reproduction, presumably maximizing longer term reproductive fitness (Harper 1977). Shade-tolerant monodominant tree species, like beech, are long-lived (Piovesan et al. 2003), and it has been demonstrated that longevity is strongly related to mast seeding in 69 temperate tree species (Waller 1979). Due to the hierarchical organization of forest structure, being dominant and large is fundamentally important for the vigorous vegetative activity that produces photosynthetate for maintenance, growth and also reproduction. Density-reduction studies have shown that in old-growth forests, large trees must also compete (Latham and Tappeiner 2002; Piovesan et al. 2005), with the result that competitive processes characterize a long part of the life span of a tree. The problem of when and how much plants should allocate to reproduction has been analyzed theoretically by several authors (see Yamauchi 1996). During cool, wet summers—favorable conditions for vegetative activity (e.g., Richardson et al. 2005)—trees grow vigorously, especially those in the upper stratum of the forest, and mature beech trees consolidate their space and accumulate reserves in sapwood. Meanwhile, in the shady environment beneath a dense forest canopy, the chances of seedling survival are low due to reduced illumination (e.g., Szwagrzyk et al. 2001). Thus, producing an abundant seed crop during a cool, rainy period would seem to be a disadvantageous resource-allocation strategy because it reduces the competitive ability of the tree (and its future reproductive fitness) and at the same time it does not guarantee the success of the offspring (i.e., seedlings). In understanding the balance between cost and benefit in masting behavior it is necessary to consider the possibilities of seedlings establishing and being recruited into the stand (e.g., Price et al. 2001). During moist years, seedlings are unlikely to establish due to competition for light from established trees: vegetative growth prevails over reproduction.

In mesic forests the rules of allocation change during a hot, dry summer; the upper stratum experiences strong drought stress to which trees respond by adapting their crown architecture and by expending reproductive effort. A hot, dry summer induces flowering and can cause profound modification in the forest stand structure. Drought stress also causes trees to abscise leaves during the growing season, leaving a more transparent crown for several years (lower leaf area index) (Bréda 1999; Le Dantec et al. 2000; Zierl 2004). In particular, fruiting beech trees have more transparent crowns (Innes 1994) because a proportion of the axillary buds have developed into flowers. This phenomenon is now well documented by the long-term monitoring program of British forests (Hendry et al. 2001), just as depression of twig extension and branch dieback following severe summer drought is documented (e.g., Power 1994). This modification of the crown architecture can in itself be an adaptation to a drought period. Due to a more transparent canopy and to the creation of gaps in the canopy as a consequence of some tree death (e.g., Beckage et al. 2000), more light arrives at the forest floor, producing a favorable environment for seed establishment and growth (e.g., Price et al. 2001; Olano and Palmer 2003). Most shade-tolerant species, like beeches, adopt the seedling-bank strategy and because seedling/sapling bank dynamics are influenced by understory light levels (e.g., Abe et al. 2005) this reproductive strategy may have advantages for advanced regeneration when the effects of the drought disturbance last for a few years. On the supra-annual time scale, a strong drought can cause not only a more open canopy as a consequence of the death of some large trees, especially those in old age, but sometimes a more general degree of dieback (Hosking and Hutchenson 1988; Innes 1992), which creates vacant patches in the forest. In birch, maple and beech stands, a generalized dieback phenomenon following a drought period and coincident with a full mast event has been observed in North America and Europe (Innes 1992). Moreover with regard to low-frequency patterns of climate, young beech trees or structural phases of the forest cycle actually survive better during a drought phase because mortality affects mainly small suppressed trees (Hosking and Hutchenson 1988; Peterken 1996), even if they do not reproduce. In this way, mature trees in effect leave enough offspring from a condition in which they waste away and die (Harper 1977). In summary, in mesic forest stands the weather cue is linked to the environmental prediction hypothesis (Selås et al. 2002; Williamson and Ickes 2002): a drought year brings about a thinning of the forest canopy lasting for 1 or more years.

Since maturing fruits are very sensitive to drought (e.g., Houle 1999), in a mesic environment after a strong drought event there is a fairly low probability of another consecutive drought. Maturing fruits are a strong carbon sink and tend to be suppressed (and/or aborted) during periods of resource deficiencies (e.g., extremely dry summer) probably to safeguard the residual reproductive fitness of the tree. One year after a drought, if the spring is mild (e.g., no late spring frost or persistent rain that damages flowering), a good masting year is the usual observed pattern (see Fig. 3 in Piovesan and Adams 2001), and a wave of regeneration may follow (Peterken 1996; Peters 1997; Abe et al. 2005).

The only proviso to this reproductive pattern is that to trigger a mast year the early summer drought must not coincide with a year with high seed production; during a mast year the endogenous control of the trees prevails over the climatic cue and stops floral induction (2 high seed years are not generally consecutive, and most seed production series are characterized by a negative lag-one autocorrelation; e.g., Kelly and Sork 2002). In this sense, in beech, a high seed year is generally preceded by a cool, moist summer 1 year prior to floral induction (mast year-2) permitting accumulation of abundant reserves in the plants (resource priming; see Fig. 3 in Piovesan and Adams 2001; see also Richardson et al. 2005). However, during fruit development the mobility of the stored carbon seems to be limited to the fruiting branch (Miyazaki et al. 2002) with some species characterized by complete carbon autonomy of fruiting at the level of whole, undisturbed branchlets (Hoch 2005). Moreover, some other studies seem to reduce the role of carbon storage in masting behavior (e.g., Stevenson and Shackel 1998). If these findings are confirmed, the endogenous control of floral induction (stimulated by suboptimal climatic conditions, Piovesan and Adams 2001) is principally due to maturing fruits (e.g., through hormones) that act to prevent another reproductive pulse the successive year; in other words during a mast year the trees generally do not respond reproductively to climatic stimuli, probably to safeguard the residual reproductive fitness of the plant. The following year, an absent (or low) production of seeds is the normal pattern causing a negative lag-one correlation in seed series. The endogenous control of reproduction is probably a factor responsible for the difference in the temporal autocorrelation between seed production and climatic series observed by Koenig and Knops (2000).

Evidence is accumulating that in forested ecosystems the environmental prediction hypothesis may have a role in a set of evolutionary hypotheses which are not mutually exclusive. Ecology must consider complex integrative systems (Berryman 2003) where a particular adaptive trait is often the product of a balance among several selective factors (see Kelly et al. 2001). Endogenous cycles, pollen limitation, predator satiation, and advantages for seedling survival under a more open canopy may work in parallel to select for masting behavior in forest trees. It should be noted that different selective disadvantages are associated with masting behavior both for parent trees (Waller 1993; Selås 2000) and seedling performance (Hett 1971). In forests, post-dispersal survival and growth of seedlings and saplings is often negatively density dependent (Wright et al. 2005), and synchronized fluctuation in seed production can cause a high density of seedlings leading to greater losses to competition, herbivory or pathogens (Kelly 1994). In addition, during low (or absent) seed years, masting trees will lose opportunities for colonization of new wind-induced gaps unless they are able to form a seedling bank such as in the case of the beech forest we have examined. The tension between these opposing forces results in complex selective pressures on the reproductive schedules of the different species that may or may not favor masting behavior. It is interesting to note that at the margin of the soil moisture gradient of temperate forests many trees do not present the masting behavior. Trees located near water courses (e.g., *Populus*, *Salix*, *Ulmus*) tend to produce high seed crops every year, probably because resources are abundant and disturbances are very frequent. The same happens (e.g., the serotinous *Pinus contorta*, Kelly 1994) at the opposite part of the gradient in the xeric sites where extreme drought periods and fires are frequent; here oak species tend to reproduce according to the nonadaptive resource-matching hypothesis (Abrahamson and Layne 2003).

We have speculated that in terms of tree ecological strategies in a mesic forest environment, a strong reproductive response following water stress (or suboptimal conditions for growth) makes sense as the original cue on which selection has worked for millions of years. It was recently suggested that, in the neotropical *Dicymbe corymbosa*, masting is a phylogenetically constrained trait of Gondwanan origin (Henkel et al. 2005). Could the same reproductive trait have been conserved in the *Fagaceae* family with reference to *Fagus* and *Nothofagus* genera or more generally in closed-forest late-successional trees? Seedling banks (advanced regeneration) and new seedling recruitment in response to a drought provide the opportunity to rapidly "colonize" (before the arrival of other species) vacant patches in the forest, a strategy that is an indisputable benefit if one considers the mosaic-cycle concept of ecosystems (Remmert 1990; Westoby et al. 2002). Studies in old-growth forests are demonstrating that late-successional saplings may endure a long suppression period under heavy shade with periods of growth linked to small gaps (e.g., Piovesan et al. 2005). Drought-induced mortality has generally received less attention than tree falls (Suarez et al. 2004), but dendrochronological studies and historical reports show that past droughts have caused extensive vegetation mortality (Allen and Breshears, in press). It was previously suggested that for investigating evolutionary and ecological processes such as mast fruiting it is important to take into consideration rare events such as droughts and to study them at the appropriate spatial scale (Curran and Leighton 2000). Because variables that affect recruitment rates interact, greater attention to spatially extensive and longer-duration sampling for early life-history stages is needed to assess the role of recruitment limitation in forests (Clark et al. 1999).

Understanding the adaptive significance of masting may require a multi-faceted approach including the study of the ecology of the trees themselves beyond pollination, and including gap ecology and patch dynamics. Generally speaking, some aspects of masting behavior are now known, but to resolve the evolutionary ecology of this reproductive strategy it is necessary to focus more on plant ecology and physiology. A fundamental question is what do seedlings die from and what are the evolutionary implications not only for seed size (Moles and Westoby 2004), but also for masting behavior? Causes of seedling mortality should be analyzed with attention to an appropriate spatial and temporal scale. So far, there are few studies on this topic that might help us to reach more general conclusions about the advantages of masting.

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