

The mast seeding plants of Bhutan

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Masting bamboo in Bhutan

Abstract

Mast seeding, the intermittent production of synchronized seed crops among plant populations, is a world-wide phenomenon that has been reported in the Himalayan mountains across a large number of habitat types, and among a wide variety of long-lived grass, shrub and tree species. In this paper, we review various hypotheses that explain why mast seeding occurs, and describe a number of

the better-known mast seeding floral elements that exist in Bhutan. We also stress the need for further documentation of the seeding cycles of plants in Bhutan, and emphasize the need for careful management of species that rely on mast seed crops for their regeneration.

Keywords: Masting, predator satiation, environmentally predictive masting, serotiny, bamboos, Bhutan, plietesial

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Introduction

Mast seeding, the intermittent production of synchronised seed crops among plant populations, is a world-wide phenomenon that has been reported in the Himalayan mountains across a large number of habitat types, and among a wide variety of long-lived grass, shrub and tree species (Janzen 1976; Negi & Naithani 1995; Singh et al. 2011). Nevertheless, in Bhutan and the eastern Himalayas in general, little is known about the ecology of local species with synchronized reproduction, and few authors appear to recognize that many Bhutanese forests are dominated by some of the world's most iconic masting plants.

This paper briefly reviews the ecology of mast seeding and describes prominent masting flora known to exist in Bhutan. In our discussion, we initially examine plants with a plietesial life history (i.e. plants that flower and set seed once in their life cycle [semelparous] and then die); and then those with an iteroparous life history (i.e. that flower and set seed numerous times during their lifetime). Where local names are indicated for plants, the abbreviation (Dz.) indicates a name given in Dzongkha, Bhutan's national language; the abbreviation (Lt.) indicates a name given in Lhotshampkha (or Nepali), the main language spoken by southern Bhutanese; (Kng.) indicates a name in Khengkha, the language of the Khengpa of central Bhutan, while (Sh.) indicates a name in Sharchopkha, a language spoken by many eastern Bhutanese. In the review, we emphasize the importance of mast seeding years for the regenerative capacity of both plietesial and iteroparous masting flora, and stress the need for further documentation and research into the phenomenon of synchronized plant reproduction within Bhutan.

What is mast seeding?

Many of the world's longer-lived plant species produce large, synchronized seed or fruit crops at intervals of greater than two years. This phenomenon is called mast seeding, after the German term for the crops of forest trees such

as beech and oak that are used for fattening livestock. While people have probably been observing and utilizing the seed crops of many mast seeding plants for much of human history, it has only been in relatively recent times that scientists have begun to try to explain how and why this phenomenon occurs.

The earliest explanation for seeding periodicity was that inter-year variation in plant reproductive output is driven by variability in resource availability, and that plants match the size of their seed crops with the weather conditions of a given year (i.e. the resource-matching hypothesis) (Busgen and Munch 1929; Kelly 1994). However, this rationalization does not explain extreme variability in seed production of 'strict' masting species such as bamboos, in which masting is strongly bimodal (with no seed produced in most years, and massive crops in some), whilst resource availability follows a more continuous distribution through time (Kelly 1994). Moreover, the resource-matching hypothesis does not explain why masting plants delay reproduction, sometimes for periods of greater than a century, given that there are costs associated with doing so. These costs include missing establishment opportunities during years of no or low seed production, and the associated risk of mortality before the next fruiting or seeding event can occur (Waller 1979; Willson 1983).

Whilst weather conditions such as precipitation and temperature undoubtedly play a proximate role in the synchronization of flowering and fruiting of many masting species (Koenig 2002), there are several hypotheses that hold that mast seeding is an evolved reproductive syndrome. The earliest and still the most widely accepted of these adaptive hypotheses is the predator satiation hypothesis (Janzen 1971, 1976; Silvertown 1980; Sork 1993). Under this hypothesis, mast seeding reduces seed predator densities via starvation during inter-mast periods, and causes them to be overwhelmed by high seed numbers during mast years. This seeding phenology enables increased numbers of seeds to escape consumption during seeding years, and improves the overall reproductive

capacity of plants by facilitating increased seedling recruitment.

Another masting hypothesis that has received wide support in the literature is the wind pollination hypothesis (Nilsson and Wastljung 1987; Kelly et al. 2001). Under this theory, synchronized flowering among outcrossing plant populations facilitates the production of large quantities of high quality seed by enhancing the likelihood of cross-pollination by wind. This hypothesis does not apply to animal-pollinated plants, and holds most firmly in low productivity environments, because when resources are scarce plants must accumulate reserves for considerable periods before being able to produce large flowering and seeding efforts (Kelly & Sork 2002). A masting hypothesis that is relevant to many fire-prone forests is the environmental prediction hypothesis. This hypothesis states that in certain ecosystems, temporally variable establishment conditions may apply selection pressure for plants to produce mast seed crops only in years that are favorable for seed germination and/or seedling establishment (Burns 2012). A precondition for the evolution of this form of masting is that an environmental cue must exist that can reliably predict these favorable future establishment conditions. Consequently, environmentally predictive masting plants may 'tune in' to such cues over evolutionary time to ensure that seeds and seedlings are produced at the most ecologically opportune time.

Whilst environmentally predictive masting syndromes have been recognized in tropical and temperate ecosystems (Williamson & Ickes 2002; Burns 2012), they are most common in fire-prone habitats (O'Dowd & Gill 1984; Wright & Zuur 2014; Wright et al. 2014). The reason for this is presumably because seedling survival in fire-dependent systems is constrained much of the time by competition and by heavy litter layers that physically and/or allelopathically impede seedling emergence, but is encouraged in post-fire situations that are low in competition, relatively free of litter, and have increased nutrient levels as the

result of combustion processes during fire (Rundel 1981).

Examples of fire-related forms of environmentally predictive masting include pyriscent serotiny and post-fire flowering. Trees with pyriscent serotiny have seed cones that synchronously release masses of wind-dispersed seeds when the resin that bonds the scales of the cones is heated during fire. Plants with post-fire flowering resprout from buried organs after fire, and produce large flower and seed crops immediately after burning. All fire-related forms of environmentally predictive masting enhance plant reproductive success by enabling seedlings to capitalize on the favorable growth conditions that exist after fire.

Mast seeding plants in Bhutan

a) Plietesimal plants

Bhutan is home to a large number of perennial monocarpic (semelparous) plants that flower synchronously at supra-annual intervals. This life history, also referred to as the plietesimal life history (Bremekamp 1944), has been observed among species of numerous unrelated plant families, including Poaceae, Arecaceae, Scrophulariaceae, Fabaceae, Apocynaceae and Acanthaceae (Daniel 2006). Plietesimal plants typically grow as an even-aged cohort for some years, and in their final year of life they flower gregariously, set seed and then die. Following dieback, a flush of seedlings emerges, and this cohort grows and repeats the cycle with an identical periodicity to that of the previous cohort. An almost indistinguishable life history is seen among mast seeding bamboos; however, the term plietesimal has not previously been applied to the phenomenon in bamboos (although it would appear appropriate for them as well).

Janzen (1976) provided important insights into the possible adaptive significance of the plietesimal life history by suggesting that the sheer abundance of seed produced during mast years is likely to overwhelm seed predators and hence increase the survival rate

of seeds and seedlings. In Bhutan, animals such as pigs, rats, squirrels and bears are known to consume the seeds of mast seeding bamboos (Dorji, S., personal communication; Mukhia, P.K., unpublished data); while in nearby India, numerous bird species (Backer 1918; Mathew 1971), rodents (Janzen 1976) and even humans (Kapadia 1950) consume the seeds of plietesial *Strobilanthes*. Thus, it is quite possible that masting in at least some of Bhutan's plietesial plants may have an adaptive link to predator satiation.

An alternative hypothesis (or additional, as masting hypotheses are not mutually exclusive) relevant to wind-pollinated bamboos is that mast flowering might improve cross-pollination in Bhutan's relatively windless understories (Janzen 1976; Stapleton, C., personal communication). Regarding the phenomenon of dieback in plietesial plants, it has been suggested that synchronized mortality after flowering may relate to favorable site conditions for seedlings following the death of parent plants (i.e. conditions that have reduced competition from adults and increased light and resource availability) (Janzen 1976;

Tsvuura et al. 2011). Nevertheless, there has been no research on any of these hypotheses in Bhutan, so an open field of investigation exists for future researchers to explore.

The plietesial life history is seen in Bhutan among a number of species within the large (350–450 species) southern Asian genus *Strobilanthes* (Acanthaceae). These shrubs and small trees are found across much of Bhutan's lower to mid-altitude regions, and members of the genus known to be plietesial in Bhutan include *S. accrescens* (Fig. 1a), *S. extensa*, *S. divaricata*, *S. echinata*, *S. helicta*, and *S. thomsonii* (Wood, S., personal communication). These species normally take between 10 and 15 years to complete their life cycle (although 12 years is the norm), and it is only in their final year that they flower and set seed gregariously. Interestingly, while many of Bhutan's masting *Strobilanthes* follow identical seeding cycles over the entirety of their range (or at least over very large areas), some species have been observed to follow quite different flowering schedules across geographically proximate regions. For example, Wood (1994) observed *S. thomsonii* flowering gregariously in 1988 in the

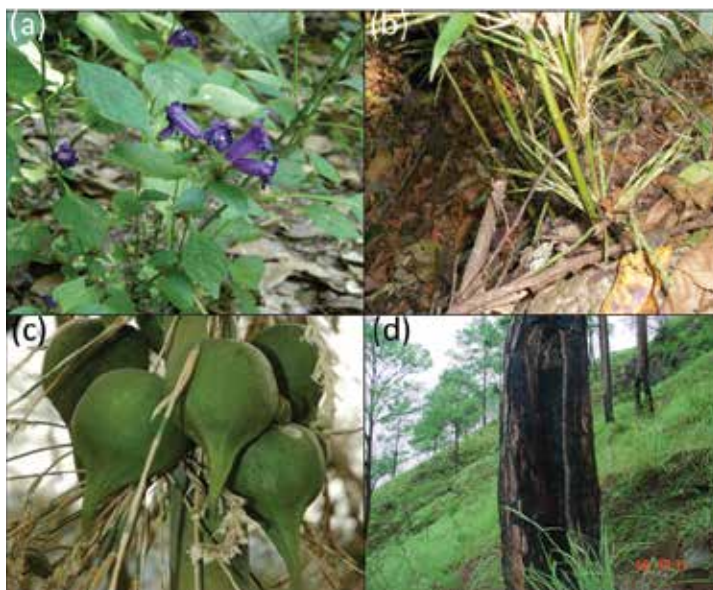


FIGURE 1 (a) The plietesial *Strobilanthes accrescens* (Photo Credit: T. Tshering); (b) inflorescences of the mast seeding *Neomicrocalamus andropogonifolia*; (c) seeds and inflorescences of *Melocanna baccifera*; (d) Bhutanese chir pine forest regenerating after fire.

Sankosh valley in central Bhutan, in 1989 in the Mangde Chhu valley near Trongsa, and in 1991 in the Dangme Chhu valley in eastern Bhutan. Another intriguing phenomenon observed among some of Bhutan's *Strobilanthes* is that populations may have a plietesial life history in some localities, but behave as non-plietesial perennials in others. For example, *S. atropurpurea* (formerly known as *S. wallichii*) and *S. auriculata* are monocarpic in the western Himalaya, but in Bhutan they flower annually and remain alive after flowering (Daniel 2006). Other *Strobilanthes* such as *S. inflata* are not known to be plietesial at all, and may flower and seed numerous times in a lifetime.

In addition to plietesial *Strobilanthes*, Bhutan is home to a number of monocarpic mast seeding bamboos. However, it is difficult to accurately state the seeding cycles of many of these species, because recording flowering cycles requires correct identification and uninterrupted observation over several human generations. Thus, for many of Bhutan's less well-known tropical species, and nearly all of the temperate ones, records for particular bamboo species are simply too short or unreliable to put a precise time frame on their inter-mast period. Even so, the masting cycles of some of Bhutan's bamboos can be tentatively inferred from brief colonial descriptions of bamboos from nearby Darjeeling and Sikkim (Munro 1868; Gamble 1896, 1912) and from more recent enumerations in Nepal and Bhutan (Stapleton 1994a, 1994b, 1994c, 1994d). For example, *Neomicrocalamus andropogonifolius* (yula [Sh.]) (Fig. 1b), a species used in the production of traditional handicrafts, may have an inter-mast period of approximately 40 years (although in certain instances this species may flower in response to environmental stresses such as drought or extreme cold, and then remain alive after flowering [Mukhia 2014]). Also, *Dendocalamus hookeri* (pagshi [Dz.]; bom bans or kalo bans [Lt.]) and many alpine Bhutanese bamboos may have inter-mast periods of up to 120 years (Gupta 1972; Janzen 1976; Stapleton, C., personal communication), and hence probably have seeding cycles that are among the longest of any of the world's masting plants.

An interesting point to make about Bhutan's plietesial plants is that although mast seeding

years are rare, they benefit both wildlife and humans by providing food and fodder. For example, in 1985–86 *Dendocalamus sikkimensis* (zhang [Dz.]; bhalu bans and dhire bans [Lt.]; demtshar or dem chherring [Sh.]; zang [Kng.]) flowered and seeded in the Samtse district in Bhutan's southern foothills (Mukhia, P.K., unpublished data). During this event, local people collected the seed to make flour for pancakes, and also produced a snack by pressing and then drying the seeds into flakes (in a similar way that pressed maize grains are used to make the traditional Bhutanese tea-time snack 'dzoau'). The regenerating seedlings of almost all mast seeding bamboos are also recognized as excellent fodder for domestic livestock such as cattle and yaks. However, because of their favorability as feed, post-dieback areas are prone to high levels of overuse and degradation (Singh et al. 2011).

In Burma, mast-flowering years of *Strobilanthes rufescens* (known locally by Shan people as 'moyan') are of economic importance, and it is believed that correct adherence to the rites of a particular bee spirit festival will ensure the perpetuation of the plants' six-year flowering cycle (C.W.A.B. 1895). As bees are among the primary pollinators of *Strobilanthes* spp., this festival and the accompanying moyan flowering years are also accompanied by increased production of economically valuable bees wax. Whether any Bhutanese folk stories exist that concern the seeding periodicity of plietesial bamboos or *Strobilanthes* would be of great academic interest, and could provide insights into the ecology of the species involved. However, as far as we know, no research on this has been undertaken.

Despite the positive benefits that mast years of plietesial species may have, local people from Bangladesh, India and Nepal view the seeding years of certain bamboos with trepidation (Belmain et al. 2010; Singleton et al. 2010). This is because the glut of seed produced during such years results in irruptions of rodent fauna that consume agricultural crops, and also cause famine and disease transmission to livestock and humans. Bamboo species of concern include the large-

seeded *Melocanna baccifera* (Fig. 1.c) (filling bans or lahure bans [Lt.]) which seeded in 2010 in northeast India and Bangladesh, and in 2007 in the Samtse district of southern Bhutan (Belmain et al. 2010; Mukhia P.K., unpublished data); and hill species, such as *Sinarundinaria falcata*, *Thamnocalamus falconeri* and *Thamnocalamus spathiflora* (hum or khom [Dz.]; rato nigalo [Lt.]; rhui [kng.]), that were observed to be seeding in the western Himalaya and Bhutan between 2001 and 2002, and 2004 and 2005 (Singh, G., personal communication; Mukhia, P.K., personal observation). Problems associated with rodent outbreaks following seeding years were effectively managed in Bangladesh using strategies such as fencing systems that incorporated multi-capture traps, and environmental programs that aimed at rodent-proofing haystacks and granaries within village areas (Belmain et al. 2010).

b) Iteroparous mast seeders

In contrast to plietesial bamboos and *Strobilanthes*, iteroparous masting plants produce numerous seed crops in their life cycle and do not die after flowering. Additionally, unlike plietesial plants in which reproductive synchrony is believed to be maintained via an internal physiological calendar (Janzen 1976), iteroparous masting plants normally rely on external weather or environmental cues to synchronize flowering (Koenig 2002). A well-known iteroparous masting plant in Bhutan is the chir pine (*Pinus roxburghii*) (they-tong [Dz.], salla [Lt.]), which dominates much of Bhutan's mid-altitude regions between 450 and 2300 masl. Chir pine has a synchronized pollen production syndrome whereby large pollen loads are released from male strobili at approximately three-yearly cycles (Khanduri 2012). As these trees are wind pollinated and primarily out-crossing, it has been hypothesized that improved wind pollination efficiency is the primary adaptive function of mast pollen production in this species. However, additional research is required to test whether this inter-annual cycle of pollen production also translates to a mast cycle in terms of cone creation (Khanduri 2012).

In addition to pollen masting, chir pine has pyriscent serotiny (the previously mentioned fire-related form of environmentally predictive masting). However, the cones of chir pine cannot be classified as strictly serotinous, because upon maturity (which takes approximately 24 months) they open gradually to slowly release small quantities of seed, and only discharge large quantities immediately after burning (Richardson 2000). This incremental seed release strategy may offer chir pine an adaptive compromise compared to more strictly serotinous species, by allowing trees to 'sample' more temporal variability in weather and environmental conditions over time, but also ensuring that maximum seed densities occur when seedling growth conditions are favorable following fire. In addition to pyriscent serotiny, a strong resprouting capacity among both juveniles and adults ensures that chir pine is well adapted to the fire-prone forests that it inhabits (Fig. 1d) (He et al. 2012).

Another important pine common to Thimphu and other regions of Bhutan is the blue pine (*Pinus wallichiana*) (tongphu [Dz.], rani salla [Lt.]). Blue pine produces good timber, is more cold resistant than chir pine, and generally occurs between 1800 and 3600 masl. While little research has been conducted on either cone production or the fire ecology of blue pine, anecdotal evidence suggests that, like chir pine, some cone production occurs annually and high production years occur with a periodicity of approximately three years (Tandin, B. unpublished data). In contrast to chir pine, however, the cones of blue pine are not serotinous, and adult trees are quite fire sensitive and regenerate primarily from seedlings after high intensity crown fires (He et al. 2012). Nevertheless, blue pine exhibits several adaptations that appear to facilitate persistence in fire-prone environments, including: i) exceptionally thick bark in mature plants (Tandin 2006; He et al. 2012); ii) juveniles with relatively strong resprouting capacity; iii) needle litter that secretes allelopathic toxins which inhibit germination of other species (and presumably reduce the likelihood of extreme high intensity fires by

decreasing fuel loads) (Forestry Nepal website n.d.); and iv) winged seeds that facilitate long-distance dispersal to fire-killed stands from trees in unburnt areas.

Another iteroparous masting group in Bhutan is the genus *Quercus* (oak trees, family Fagaceae). *Quercus semicarpifolia* (Kharsu oak [Lt.] or bji shing [Dz.]), which is one of the main evergreen species in Bhutan's temperate to sub-alpine regions (2500–3300 masl), is reported as having a mast seeding cycle of approximately 8–10 years, and during mast years seed production can be up to ten times greater than in non-mast years (Negi & Naithani 1995). The escape of seeds during mast years from seed predators such as bears, Himalayan tahr, barking deer and monkeys such as Hanuman langurs and the rhesus macaque has led researchers to conclude that predator satiation is likely to have played an important role in the evolution of oak mast seeding in the Himalaya (Negi & Naithani 1995; Singh et al. 2011). Other Bhutanese oaks include *Q. griffithii* (sisi shing [Dz.]), *Q. glauca* (thomp [Dz.]), *Q. lamellosa* (dhom sokey or Bangka [Dz.]), and *Q. lanata* (ghoom [Dz.]). However, monitoring is required to determine whether these species are mast seeders as well.

In many Himalayan regions, natural regeneration following mast years of certain tree species has been greatly reduced by factors such as overgrazing by migratory pastoralism, fodder collection, anthropogenic burning and unmanaged tourism (Singh et al. 2011). In places, these disturbances have been so intense that it has been only within the protected thickets of bamboos such as *Sinarundinaria falcata* (Himalayan dwarf bamboo) and the high altitude bamboo *Yushania microphylla* (mingma [Dz.]) that regeneration of mast seeding trees such as oaks and conifers such as *Abies densa* (Pinaceae) has actually occurred (Gratzer et al. 1999; Singh 2000). As a result, Singh et al. (2011) have emphasized the need for careful management by government authorities and pastoralists to ensure adequate regeneration of mast seeding plants during mast years. At present, however, we are aware

of no previous research conducted in Bhutan that has assessed the impacts of anthropogenic factors on the regeneration of masting plants. It therefore seems expedient that such research shortfalls should be addressed promptly.

Another issue of concern for Bhutan's iteroparous masting flora is the impact of climate change on masting cycles. Plants such as oaks and *Pinus* rely on abiotic cues, including temperature and precipitation (or drought), to synchronize reproduction among populations (Perez-Ramos et al. 2010). In the Himalaya, climate change is projected to result in increased temperature and monsoon-driven precipitation, but decreased precipitation during winter (Gautam et al. 2013). Such changes may alter the frequencies of mast years for species that rely on rainfall or temperature changes to synchronize reproduction. However, researchers have cautioned that predicting the actual impacts of climate change on masting flora will not be clear cut, as increased masting frequencies could also increase population densities of predator species that feed on mast seed crops (and hence reduce or eliminate the predator satiation benefits of mast seeding) (Iler & Inouye 2013). Consequently, whilst changes to the seeding cycles of at least some of Bhutan's masting flora appear imminent, predicting the effects of climate change on the regeneration dynamics of mast seeding species will be complex and probably site-specific.

Conclusion

Many of Bhutan's dominant canopy and understorey flora are mast seeders that produce large synchronized seed crops at intermittent intervals. However, we suggest that many more masting species may be identified if long-term monitoring and research on the phenological patterns of Bhutanese plants is undertaken. This information will further bolster understanding of the complex ecology of Bhutan's precious forests, and is critical to understanding the potential effects of climate change on the reproductive cycles of plants that rely on weather cues such as temperature, precipitation or snowfall to initiate mast seed production events.

Within Bhutan's known masting vegetation, there is a range of possible adaptive reasons that may explain why seeding periodicity has evolved, including improved wind pollination efficiency by bamboos and some conifer species, predator satiation by oaks and bamboos whose seeds are consumed by animals, and the prediction of post-fire periods favorable for seedling establishment (*Pinus* spp. with pyriscent serotiny). In other parts of the Himalaya it has been observed that natural regeneration following mast years has been reduced by overgrazing, anthropogenic burning and unmanaged tourism. While there is presently no evidence of these problems in Bhutan, additional research is needed to document the ecology of mast seeding plants and assess whether anthropogenic activities are adversely affecting regeneration of masting vegetation. If climate change or anthropogenic activities are negatively impacting regeneration of masting species, it may be necessary to identify and develop management strategies to ensure the survival of these important components of Bhutan's flora.

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