

Notes and Comments

Mast Flowering and Semelparity in Bamboos: The Bamboo Fire Cycle Hypothesis

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Redstick is whippin' um up like a canebrake fire. (Fess Parker in *Davy Crockett, King of the Wild Frontier*, 1955)

Mast flowering is the phenomenon of massive flowering and fruiting at intermittent intervals that is synchronized within a species across large areas. Most masting species are iteroparous, flowering and fruiting multiple times during their life span (Silvertown 1980). Bamboos are an exception as mast flowering is largely restricted to semelparous species that flower once and die (Janzen 1976). Additionally, whereas most mast-flowering species produce seed crops on a cycle of 3–7 yr (Silvertown 1980), bamboos have intermast intervals that are typically an order of magnitude longer.

The earliest explanation for mast flowering in bamboo was that of external controls on physiological processes by available resources such as rainfall (Brandis 1899), the resource-matching hypothesis. Today, this bottom-up hypothesis largely has been replaced by top-down explanations involving pollinators and predators (Kelly 1994). It is widely accepted that the selective force driving the evolution of masting in bamboos is “predator satiation” (Janzen 1976; Gadgil and Prasad 1984; Kelly 1994). This hypothesis proposes that irregular fruiting cycles are sufficient disequilibrium to inhibit seed predators from main-

taining populations large enough to decimate a “mast year” of fruiting. Predator satiation also has been invoked to explain masting in many other species (Kelly 1994) and to explain intraseasonal and interannual reproductive synchrony in both plants and animals (Ims 1990).

We contend there are features of the bamboo life cycle that weaken the case for predator satiation as an important selective force, in particular the very long intermast periodicity and monocarpic reproduction. Here we present a new hypothesis that accounts for masting, semelparity, and delayed reproduction in bamboos and provides a mechanistic model to explain variation in intermast periodicity.

The Bamboo Life Cycle

Of the nearly 1,000 bamboo species (Poaceae: Tribe Bambusae), masting is largely restricted to woody species, distributed in subtropical and temperate evergreen or deciduous forests (Soderstrom and Calderón 1979). India has one of the highest concentrations of mast-flowering species—70 of 72 bamboo species (Gadgil and Prasad 1984), but mast-flowering bamboos are found throughout Asia, Africa, and the Americas (McClure 1966).

These bamboos have aggressive rhizomatous growth and form large clonal clumps that may cover hundreds of square meters, usually in close juxtaposition with other conspecific clones, a feature contributing to the often used phrase “gregarious flowering” (Blatter 1930). The large clonal patches preempt space and greatly inhibit seedling recruitment (Veblen 1982, 1989; Taylor 1987; Peters et al. 1992; Taylor and Qin Zisheng 1992; Pearson et al. 1994; Hiura et al. 1996; Kitzberger et al. 1997; Koichi 1997; Platt and Brantley 1997; Widmer 1997). Most bamboos in both the Old World and New World are seral, and, in the absence of disturbance, clones decline owing to canopy closure, a successional cycle that takes 50–200 yr (Kerfoot 1964; Joshi 1975, 1980; Numata 1979; Rao and Ramakrishnan 1987; Young 1990, 1996; Widmer 1997).

Mast-flowering bamboos are long lived, typically 20–60 yr, but some exceed 100 yr before flowering and dying

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(Janzen 1976). There are reports of phenomenal species-wide synchrony, but the norm is generally for more localized regions of masting (10^3 – 10^5 ha) that often spread wavelike from year to year across the landscape (Brandis 1899; Henkel 1927; Blatter 1930; Win 1951; Gadgil and Prasad 1984; Taylor et al. 1991; Banik 1995). Thus, populations of the same species may not mast at the same time or even with the same periodicity. Within a region there is no firm evidence that species flower at precisely the same interval each flowering cycle. During a masting event, flowering is commonly spread over more than a single year (Kawamura 1927; Hossain 1962; Veblen 1982; Gadgil and Prasad 1984; Banik 1995; Widmer 1997). Despite this, the very long periods of no flowering between masting events results in an extraordinarily high annual variance in seed output; thus, according to Kelly (1994), bamboos come the closest to “strict masting” of all the masting species.

Most mast-flowering bamboos are semelparous, and all semelparous species are mast flowering. A few species do not die after flowering, and there are isolated cases of survivorship for normally semelparous species (Janzen 1976). Postfruiting mortality includes death of regenerative ability in belowground rhizomes, which is surprising in light of the extraordinary regenerative powers of these rhizomes (McClure 1966; Wong 1991), and their ability to survive repeated harvesting of culms (Isagi et al. 1997).

Most mast-flowering bamboos have passive dispersal, concentrating seedling recruitment near the dead skeleton of the parent plant (Brandis 1899; Kadambi 1949; McClure 1966; Fanshawe 1972; Gadgil and Prasad 1984; Taylor et al. 1991; Taylor and Qin Zisheng 1993; Widmer 1997). Seedling recruitment in many species suggests a bet-hedging strategy in which germination is spread across 1–5 yr (Blatter 1930; Fanshawe 1972; Taylor and Qin Zisheng 1988; Taylor et al. 1991). Factors controlling seed dormancy are unknown.

Semelparity and Delayed Reproduction Theory

Factors driving the evolution of semelparity have long attracted attention, but, despite the fact that Cole (1954) could find little theoretical justification for iteroparity, most articles have focused on the unusual circumstances surrounding the evolution of semelparity (Young and Augspurger 1991). Charnov and Schaffer (1973) revisited Cole's paradox and concluded that the gain in intrinsic growth rate achieved by switching from semelparity to iteroparity was equal to adding P/C individuals to the average clutch size of a semelparous organism, where P and C equal adult and juvenile survivorship, respectively. Thus, semelparity is expected in environments where adult sur-

ivorship is low, relative to seedling survivorship, a conclusion supported by other models (Takada 1995).

Although originally formulated in terms of annual survivorship, this conclusion may apply to bamboos if we consider mast-flowering cycles (t) as a metaphor for annual cycles. Let $N_{(t+1)} = \lambda N_t$, where λ is population growth rate. If semelparity (s) and iteroparity (i) were of equal reproductive value, then $\lambda_s = \lambda_i$ and $B_s = B_i + P/C$, where B is equal to seedlings per adult clone and P and C are adult clone and seedling survival, respectively.

This points to several factors that could drive the evolution of semelparity. As previously recognized (e.g., Janzen 1976), high seedling recruitment and survivorship could favor semelparity. Equally important, however, is reduced survivorship of clones between mast-flowering events.

Young (1981) pointed out that Charnov and Schaffer's conclusion is dependent on the ratio of prereproductive development time to the time between reproductive events. In bamboos, this ratio equals unity, and periodicities between flowering events are long, factors that would favor semelparity and indicate a link between delayed reproduction and semelparity.

Delayed reproduction is expected if the reproductive success : effort ratio increases with age (e.g., Gadgil and Bossert 1970; Schaffer 1974)—for example, if a long prereproductive period is required to accumulate sufficient carbohydrate stores to support mass flowering (resource allocation hypothesis). An alternative theory for time-varying environments (Charlesworth 1980) is that early reproduction should be avoided if chances of successful seedling recruitment are increased by changes in environmental conditions that are tied to adult longevity (habitat modification theory; Stearns 1980). For example, if seedling success was precarious during the early growth phase of a clone but increased following expansion of the parental clone, then delaying reproduction until significant space had been preempted by the parent plant would be of selective value.

These two hypotheses for delayed reproduction predict different causal mechanisms for adult mortality and link delayed reproduction to semelparity in different ways. The resource allocation hypothesis considers postfruiting mortality to be the result of exhaustion of resources. In contrast, if the selective basis for delayed reproduction is tied to the direct effect of habitat modification on seedling success, and mortality of the parent plant further enhances the habitat, death may be triggered by senescence hormones, even if resources are not exhausted (Noodén et al. 1997; Wilson 1997).

Hypothesis

In bamboo, the combination of mast flowering, semelparity, delayed reproduction, and gregarious distribution are all essential components of a character syndrome that contributes to enhanced fitness in a forest species dependent on canopy gaps for persistence of clones and for seedling recruitment.

A predictable gap-forming disturbance in subtropical and temperate forests is wildfire. In these ecosystems, landscape patterns of burning are a function of fuel loads and climate (Clark 1990; Bond and van Wilgen 1996). Although climate is beyond the control of any species, plants can affect fuel loads and thus increase the probability of disturbance (Mutch 1970), and disturbance-prone plant species may evolve characteristics that increase flammability (e.g., Rundel 1981). For this to enhance inclusive fitness, postfire recruitment or subsequent survival must be increased for the flammable species and reduced for less flammable neighbors (Bond and Midgley 1995).

We hypothesize that mass mortality in postfruiting bamboos generates a widespread and synchronous fuel load that significantly increases the potential for wildfire disturbance. Also, the dense monospecific “gregarious” aggregations of bamboo increase the effective target area to collect lightning strikes and thus increase the probability of ignition (Wardle et al. 1997). Further, we propose this effect has been of sufficient advantage to select for the semelparous life history. This strategy increases the chances for canopy disturbance, which both increase resources for seedling recruitment and resets the successional cycle to favor persistence of the new clones. Since the advantages of increased flammability have a restricted spatial scale of influence, localized seed dispersal in bamboos is consistent with inclusive fitness theory.

In such a system, clones could be selected to “cheat,” by not dying and by evolving propagules that disperse to the vicinity of dead clones. Selecting against these attributes is the likelihood that they would jeopardize both short- and long-term success. In the short term, seedlings of “cheaters” would have limited survivorship in competition with the parent clone, and if dispersed to the shadow of dead clones, they would be greatly outnumbered by locally dispersed seeds of that clone. In the long term, “cheater” clones would be less likely to promote disturbance and eventually succumb to canopy closure. It is noteworthy that postflowering death, including loss of rhizome regeneration, is an aspect of the bamboo life cycle that is shared with species in other fire-prone environments, where resprouting has been replaced by an obligate-seeding strategy (Bond and van Wilgen 1996; Keeley 1999).

The Bamboo Wildfire Cycle

Mast-flowering bamboos are distributed in many subtropical and temperate forests that experience a 3–7-month dry season, often punctuated by wildfires. In monsoon forests of India (Brandis 1899; Kadambi 1949; Yadav 1963; Joshi 1975, 1980; Rao and Ramakrishnan 1987; Sharma and Rikhari 1997) or Southeast Asia (Win 1951; Stott 1986, 1988; Stott et al. 1990), lightning storms at the end of the dry season result in a predictable fire regime of low-intensity surface fires that erupt into high-intensity fires where fuel loads are high.

In temperate bamboo forests of China (Taylor and Qin Zisheng 1992), Africa (Kerfoot 1964; Fanshawe 1972), Japan (Oshima 1961; Franklin et al. 1979), North America (Platt and Brantley 1997), Central America (Horn 1990; Middleton et al. 1997), and South America (Veblen et al. 1992), fires are less frequent but more catastrophic. In these regions, synoptic weather conditions conducive to lightning formation may occur only once or twice a decade and fires only once or twice a century (Kitzberger and Veblen 1997; Kitzberger et al. 1997).

Although contemporary patterns of wildfire have been greatly altered by humans, historical records of bamboo forests do support a strong linkage among synchronized mortality, fire, and bamboo recruitment. For example, in India, Brandis (1899, p. 4) reported that following the 1859 mast flowering of *Bambusa polymorpha*, “the jungle fires of March, April and May subsequently swept away the tangled masses of dry stems, and after the rains of 1861, the ground everywhere was covered by millions of seeding bamboos, which soon grew up into slender plants, 2 to 3 feet high, forming dense waving green masses on the ground under the trees.”

For another Indian bamboo species, Kadambi (1949, p. 290) described, “Fierce forest fires followed the death of the bamboo [*Dendrocalamus strictus*] to be accompanied almost immediately thereafter by copious natural regeneration. ... Every gregarious flowering and death of bamboos ends in causing disastrous fires whose ravage is often indescribable; wholesale destruction or at least crippling of the forest tree stand.” Similar accounts of a linkage between bamboo mortality and wildfires are reported for other species in India (Bourdillon 1895; Gadgil and Prasad 1984), Africa (Henkel 1927), North America (Platt and Brantley 1997), and South America (Kitzberger et al. 1997).

At the landscape scale, bamboo fuel loads are phenomenal owing to the size of clones (genets), density of culms (ramets), and culm size (5–50 m tall), which generate dry weight fuel loads of $10\text{--}10^5$ kg ha⁻¹ or more (Fanshawe 1972; Veblen et al. 1980; Pearson et al. 1994; Isagi et al. 1997). Structurally, these fine fuels have characteristics that

enhance flammability, and their high caloric content results in “explosive” ignition (Stott 1988; Platt and Brantley 1997). Because of their great height or climbing aspect, dead bamboos act as ladder fuels capable of spreading fire to adjacent canopy trees. These fuel characteristics, coupled with a seasonally dry climate and weather patterns that generate lightning ignitions, place many bamboo communities among the most fire-prone ecosystems. Circumstantial evidence that mass mortality of bamboos would increase the probability of wildfires is the statistically significant correlation between hurricane disturbances and fire in the southeastern United States (Meyers and van Lear 1998) and subtropical rain forests of Queensland (Webb 1958), where massive fuel accumulation from storm damage makes these ecosystems susceptible to subsequent wildfires.

The bamboo fire cycle hypothesis does not require precise timing of mortality and ignition, as fuel loads will persist for some time, the length of which likely varies from 2 to 3 yr in subtropical regions (Kwe-Tu-Wet-Tu 1903) to 5 yr or more in temperate forests (Makita 1997; J. E. Keeley, personal observations). Many populations flower over a period of 1–3 yr. If fires occur during the early stages of this period, nonflowering clumps will readily resprout after fire, flower, and then die (Bradley 1914).

In many species, germination is staggered over several years, thus providing a temporal window over which fire can occur. This bet-hedging germination strategy takes advantage of the unpredictable concordance of mortality and ignitions and appears to be more common in temperate forests where fires are likely controlled by weather patterns that may not form every year. On the Indian subcontinent, where annual lightning ignitions are more predictable, species appear to have limited seed dormancy. In the event seeds germinate prior to fire, seedlings have the capacity to resprout owing to the early formation of deeply placed rhizomes (Brandis 1899; Hossain 1962; McClure 1966; Fanshawe 1972). Indeed, bamboo seedlings will resprout under fire intensities that kill associated tree seedlings (M. Gadgil, personal communication).

Model of Flowering Periodicity

Bamboos differ greatly in the length of time reproduction is delayed. We support the idea that flowering periodicity is controlled by a genetic clock but suggest that developmental and ecological factors have played a selective role in setting that clock. Our hypothesis leads to predictions about masting cycle periodicity that we contend is a function of the rate of canopy tree invasion into gaps and the rate of bamboo maturation. Although bamboo clones inhibit tree recruitment, they are not immune to invasion (Numata 1979; Joshi 1980), and we predict that,

as the rate of canopy tree invasion increases, selection favors a decrease in the length of time between masting events. On the other hand, as maturation rate declines, we expect flowering periodicity to increase. This could be driven by two factors. As growth rate declines, the time required to accumulate biomass sufficient to carry a fire into the forest canopy increases. Also, as the rate of resource accumulation declines, the time necessary to accumulate sufficient resources for a mast-flowering event increases (Taylor et al. 1991).

Qualitative predictions (fig. 1) about flowering periodicity are based on the intersection of the reciprocal of the maturation curve and the curve describing probability of invasion. The shapes of the curves for both maturation and invasion are speculative. For example, some have suggested bamboo growth curves are linear (Oshima 1961; Isagi et al. 1997), whereas others have documented exponential growth curves (Gadgil and Prasad 1984). Probability of tree invasion is assumed to be related to rates of gap closure and canopy tree recruitment, and thus curves are likely to vary with the forest type. The model predicts the shortest masting periodicity for environments with rapid tree invasion and rapid bamboo maturation and the longest periodicity for environments with slow invasion and maturation.

As predicted by our hypothesis, the most widespread bamboo species, *Dendrocalamus strictus*, exhibits extraordinary levels of population variation in flowering behavior (Brandis 1899; Kadambi 1949; Banik 1995), in a manner consistent with our model for flowering periodicity (fig.

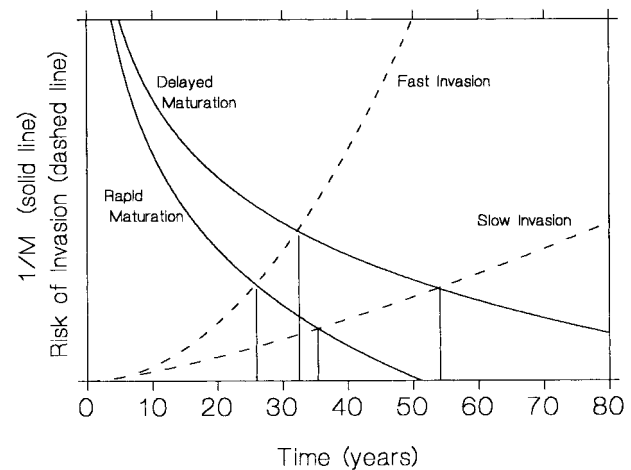


Figure 1: Model relating flowering periodicity to rates of tree invasion and the inverse of bamboo maturation. The shortest masting periodicity is predicted for environments with rapid invasion and rapid maturation, and the longest periodicity is predicted for environments with slow invasion and slow maturation.

1). Since growth rate of both bamboo and invasive trees is likely to be controlled by water balance (the interaction of water and energy; Stephenson 1990), within a region such as India, this parameter should be correlated with precipitation. As precipitation increases, bamboo maturation and tree invasion should be more rapid, thus leading to a prediction of shorter periodicity in flowering (fig. 1); limited data available for this species support this prediction (fig. 2). Additionally, in the arid, more severe parts of this species' range, mast flowering is replaced by sporadic flowering behavior (Nicholson 1922; Campbell 1985), consistent with predictions when maturation and invasion curves fail to intersect (fig. 1).

On a continental scale, flowering periodicities between species also are consistent with predictions from our flowering periodicity model (fig. 1). Higher temperatures at lower latitudes would be expected to increase rates of bamboo maturation and tree invasion and thus decrease periodicity, and this is the pattern across Indo-Asia (Campbell 1985). Also consistent with our model of flowering periodicity is the fact that understory species, with the slowest growth rates, have the longest masting cycles, often exceeding 100 yr (Kawamura 1927; Makita 1997).

We expect regional patterns of disturbance play a selective role in determining flowering behavior. For example, fires are rare in the rain forests of Malaya and the Neotropics, and the rich bamboo flora of these regions lacks synchronized flowering (McClure 1966; Holttum 1967). In habitats where other disturbances such as flooding, snow pack, or treefalls are common, we predict diminished importance of mast flowering.

Alternative Hypotheses

The fire cycle hypothesis explains life-history characteristics of bamboo better than alternative hypotheses proposed for mast flowering. The predator satiation hypothesis (Janzen 1976) has several weaknesses. First, the extraordinarily long flowering periodicity far exceeds the life span of the most common seed predators and would not be required to control predator populations. Second, the relatively localized scale of masting typical of bamboos would allow larger seed predators to migrate from one masting population to another in subsequent years, favoring growth of predator populations. Third, during a "masting" event, flowering is often spread over more than a single year, allowing nonmigratory predators to capitalize on subsequent seed production. Fourth, at a regional scale, there is a statistically significant tendency for the mast flowering of different species to cluster together over a period of 10–15 yr (Campbell 1985), which would tend to sustain predator populations. Finally, seed germination

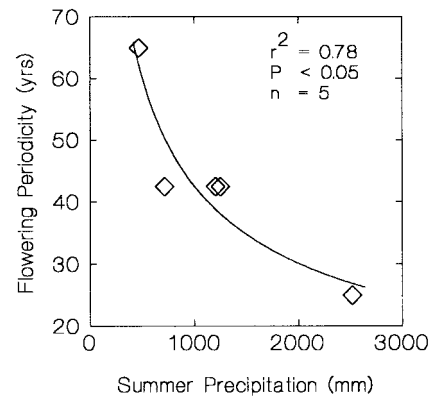


Figure 2: Observed flowering periodicity for bamboo *Dendrocalamus strictus* in different regions of India versus regional monsoon precipitation patterns; flowering cycles from Banik (1995) and precipitation data from Joshi (1975).

is often spread across several years, which would favor predator populations.

Postfruiting mortality is a necessary feature of the bamboo fire cycle hypothesis and may result from either exhaustion of resources or be induced by senescence hormones. In contrast, top-down hypotheses involving predators and pollinators (Kelly 1994) do not consider semelparity to be adaptive, and thus mortality must result from an exhaustion of resources. However, there is evidence suggesting resources may not be depleted by flowering. Sexual reproductive effort has been calculated, in one species, at 20% of total biomass (Gadgil and Prasad 1984), which is not beyond that of perennial iteroparous grasses (Fitter 1986) and may be less than the annual allocation to bamboo rhizomes (Campbell and Qin Zisheng 1983; Isagi et al. 1997). Another observation inconsistent with this mechanism is that clones failing to mature fruits also die (McClintock 1970; Taylor and Qin Zisheng 1988). In addition, two reports note that substantial quantities of soluble carbohydrates remain in culms following fruiting (Lowrie 1900; Win 1951), which suggests that resources have not been depleted during flowering.

Another hypothesis for mast flowering proposes that bamboo mortality is a mechanism for escaping parasites (Pearson et al. 1994). However, localized seed dispersal produces very little change in the spatial distribution of bamboo populations, and thus there is limited likelihood of escape from parasites, unless, of course, mortality were coupled with burning of dead debris (soil-sterilization hypothesis), which would accompany wildfires.

Some lesser-known hypotheses have proposed an adaptive role for linking reproduction and mortality but differ from our hypothesis in arguing that mortality alone is of

selective value, because it increases resource availability for bamboo seedlings (Simmonds 1980; Gadgil and Prasad 1984; Taylor and Qin Zisheng 1993; Clark 1997). The primary deficiency with this "ecological release" hypothesis, as we call it, is that bamboo mortality, in the absence of disturbance, leads to greatly enhanced tree recruitment (Numata 1979; Taylor 1987; Taylor et al. 1991; Taylor and Qin Zisheng 1992, 1993; Makita 1997; Widmer 1997) and rapid weed invasion (Win 1951; Rao and Ramakrishnan 1987), both of which reduce bamboo seedling recruitment.

A limitation common to all hypotheses other than the bamboo fire cycle hypothesis is that in the absence of disturbance, successional changes result in the decline of bamboo populations (Franklin et al. 1979; Nakashizuka 1991; Peters et al. 1992; Taylor and Qin Zisheng 1992; Young 1996; Makita 1997). Seral or gap-phase species are dependent on linking reproduction to disturbance, typically through annual reproduction (even in woody species) and long-distance dispersal (Harper 1977). Bamboos would seem to "violate all the rules" in having reproductive events widely separated in time, coupled with weakly dispersed seeds. Our hypothesis contends that bamboos, unlike other seral species that seek out disturbance through frequent reproduction and widely dispersed seeds, create conditions that bring disturbance to them and coordinate reproduction with these conditions.

The bamboo fire cycle hypothesis bears some resemblance to the explanation proposed for semelparity in the tropical rain forest canopy tree *Tachigalia versicolor*. Foster (1977) proposed that semelparity could be an advantage because the fallen parent would create gaps, or safe sites for seedlings. Although not having population-level masting cycles, *T. versicolor* has some synchrony in that a small proportion of the population flowers and dies in the same year, following a several-year hiatus of no flowering in the population. Reproductive synchrony likely enhances cross-pollination, but it does not appear to increase the probability of disturbance, as proposed by the bamboo fire cycle hypothesis.

Another sort of limitation to previous hypotheses of masting is that they fail to provide a conceptual framework for explaining vastly different flowering periodicities between species. The bamboo fire cycle hypothesis provides a mechanistic basis for understanding different mast-flowering intervals (fig. 1).

Conclusions

The bamboo fire cycle hypothesis effectively links mast flowering, semelparity, delayed reproduction, and the typically gregarious distribution. Delayed reproduction and semelparity generate massive amounts of fuel, and the gregarious clonal distribution produces a contiguous fuel

load, all of which encourage the propagation of high-intensity fires. This effectively eliminates canopy trees and canopy tree recruitment. Mast flowering synchronizes seedling recruitment with the creation of safe sites in canopy gaps. Semelparity, in addition to setting the stage for disturbance, also concentrates reproductive allocation to the optimum time for recruitment.

Although the bamboo fire cycle hypothesis explains life-history characteristics more completely than alternatives, this hypothesis is not mutually exclusive of other factors playing a selective role in the evolution of this complex response. While not ruling out the origin of this syndrome in a single punctuated step, scenarios involving stepwise changes may be more parsimonious. Arguing in favor of what we termed the ecological release hypothesis, Gadgil and Prasad (1984) contended that semelparity preceded the evolution of masting in bamboos. Under the bamboo fire cycle hypothesis, evolution of semelparity would confer limited advantage in the absence of the widespread synchrony that accompanies mast flowering; thus, we view mast flowering as setting the stage for the subsequent evolution of semelparity. Mast flowering alone could have selective value (e.g., enhanced pollination; Clark 1997) and may have persisted for some time in the absence of semelparity. Indeed, some mast-flowering bamboo species survive flowering and are iteroparous, whereas all semelparous species are also mast-flowering plants (Chapman 1997). A likely site for the origin of semelparous bamboos would be the ecotone between forests and savannas, a habitat occupied by many contemporary bamboo species. As is observed today, the enhanced fuel load created by mast flowering and mortality of ecotonal populations of bamboo carries frequent grassland fires into the forest, expanding the seedbed for seedling recruitment (Stott 1986, 1988).

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