The Bamboo Fire Cycle Hypothesis: A Comment

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The bamboo fire cycle hypothesis proposed by Keeley and Bond (1999) argues that lightning-ignited wildfire has synchronized flowering and recruitment of bamboos throughout Asia. They argue that mast flowering followed by mass mortality leads to fuel-load accumulation, encouraging ignition by lightning strikes that results in complete consumption of litter and dead stalks, which both enhances bamboo regeneration from seeds and seedlings and simultaneously suppresses neighboring vegetation. They further argue that such fires create the conditions for monocarpic (semelparous, or breeding only once) reproduction of clones at long intervals, a feature that distinguishes woody bamboos from other bamboos and from the vast majority of higher plants.

We do not find the hypothesis compelling. Multiple causation is the rule in ecological and life-history explanation (Quinn and Dunham 1983), and it is always possible that fire has played a role in the evolution of some bamboo taxa somewhere. But we see no evidence that fire has played a central role in the evolution of mast flowering or monocarpy in general or in our area of direct experience in South Asia, where 70 of 72 woody bamboo species are monocarpic and mast flowering (eight species are strictly synchronous; see Gadgil and Prasad 1984; Kelly 1994). We do not see evidence that other plant taxa are fire adapted in habitats where mast-flowering, monocarpic bamboos thrive nor do we find the logic of the argument convincing on its merits. Aspects of bamboo biology remain puzzling, but we are forced to conclude that whatever resemblance highly seasonal monsoon forests of Asia have to fire-prone and fire-adapted ecosystems of the world is superficial and that such other explanations for mast fruiting as seed-predator satiation still explain the evidence better than the bamboo fire cycle hypothesis.

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Bamboo Geography and Evolution

Woody bamboo species belonging to the subtribe Bambuseae are characterized by long flowering cycles with monocarpic reproduction (reproduction once, followed by death) that separates them from herbaceous bamboos and the vast majority of higher plants (Soderstrom 1981). Exceptions occur, with some herbaceous genera (e.g., *Olyra*) showing mast flowering and monocarpy and with some woody bamboo species from the Americas and Asia showing monocarpy but also continuous flowering with only a small percentage of individual clumps in bloom at one time (Janzen 1976; Gadgil and Prasad 1984; Judziewicz et al. 1999). The bamboo fire cycle hypothesis hopes to explain woody species that flower and seed synchronously and die shortly thereafter.

Available molecular and morphological evidence indicates that woody bamboo species evolved from herbaceous allies in humid forests of the Southern Hemisphere during the Cretaceous (70–140 m.y.b.p.; Clayton 1981; Hsiao et al. 1999; Judziewicz et al. 1999). Extant herbaceous bamboos occur in New World rain forests. The basal lineage within the herbaceous bamboos is *Buergersiochloa*, which is restricted to the rain forests of New Guinea (Judzeiwicz et al. 1999). In the Old World, woody bamboos are present in tropical nondeciduous, temperate nondeciduous, semideciduous, and monsoon forests of Southeast Asia, Africa, Madagascar, and tropical North Australia. The center of woody bamboo diversity in the Paleotropics is in tropical and temperate nondeciduous forests of Southeast Asia. Diversity is low in Africa and Australia. In the New World, the highest diversity and greatest degree of endemism are in the Atlantic humid and littoral forests of Brazil, the north and central Andes, Mexico, and the Guyanan highlands (Soderstrom 1988; Clark 1990, 1995). Some woody bamboo species are present in dry and fire-prone habitats in the southwestern United States, the Brazilian cerrado, and the deciduous forests of Asia and temperate South America, where underground meristems and their ability to reproduce vegetatively from rhizomes make adult plants resistant to fire, but most are plants of the humid Tropics. One hoping to explain existing bamboo biology must explain how mast-flowering, monocarpic species fare in humid tropical, temperate nondeciduous, and monsoon habitats, where the vast majority of taxa reside and from which they apparently evolved. Evolution in the humid tropical forests of the Southern Hemisphere does not suggest that fire influenced long flowering cycles that are thought to have evolved early. We know of no evidence of a cyclical weather pattern that consistently involves lightning that is not followed by heavy rain in these humid, equatorial climates.

History of Vegetation in India

India is of some interest because it is mentioned prominently by Keeley and Bond (1999) due to the fact that almost all of its resident woody bamboos flower more or less synchronously (see Kelly 1994) and because its highly seasonal monsoon climate is common throughout South and Southeast Asia. If the bamboo fire cycle hypothesis has validity, it should be apparent in lowland forests of South Asia.

It is tempting to consider the extremely dry intermonsoon season in which forest understories are repeatedly swept by anthropogenic fires as comparable to dry summers in fire-prone habitats like the southeastern or northwestern coniferous forests of the United States (e.g., Platt et al. 1991) or to the tallgrass prairie savannas of central North America (Noss et al. 1995) that have now disappeared. This is especially tempting for one of us (H.F.H.) who disputes the contention by early observers that most fires in tallgrass systems were caused by indigenous peoples (see Higgins 1986) rather than by lightning (Higgins 1984; Howe 1994). However, similarities are superficial. While lightning strikes are frequent in the affected areas of North America (e.g., Komarek 1968), they are not known to occur unless accompanied by heavy rain in the Indian monsoons (Orville and Henderson 1986). Fire is common in seasonal deciduous monsoon forests in India, but it is widely known to be anthropogenic by ecologists (Gadgil and Meher-Homji 1985; Singh et al. 1985) and by the villagers who set the fires. While fuel builds up over seasons without fire in temperate ecosystems, litter completely decomposes during the Indian monsoons, leaving bare earth (S. Saha, unpublished manuscript). While dominant vegetation in fire-prone temperate habitats is clearly adapted to and resistant to fire (e.g., Whelan 1995), no such obvious adaptations are evident in the monsoon forests; there is no evidence of serotiny, postfire-obligate seeding, or other hallmarks of fire-adapted ecosystems (Whelan 1995). Sprouting from damaged shoots is becoming increasingly prevalent in these forests as clonal species replace nonclonal ones under the influence of recent and contemporary anthropogenic practices (S. Saha, unpublished manuscript), but sprouting is a general adaptation to damage from herbivory, drought, windthrow, fire, or other causes (Trabaud 1987) and is evidently much more prevalent now than in recent decades. While flammable targets are all but gone from the former eastern tallgrass prairie (which has now been converted to corn and soybean fields), flammable litter accumulates so rapidly in Indian forests that people often set fire to them several times a dry season. If lightning existed, there would be something to ignite and many people to witness the ignition. The issue is that despite wide areas of ample fuel, lightning unaccompanied by heavy rain is unknown in habitats that are home to a high diversity of synchronous, monocarpic bamboos.

If lightning-ignited wildfire is now uncommon in Indian monsoon forests, it was far less likely in the past (see Valdiya 1999). From the late Cretaceous (70–80 M.Y.B.P.) onward, the Indian landmass experienced a tropical equatorial climate comparable to the wet lowlands of Africa, Asia, and South America today. The Palaeocene flora of peninsular India is probably parental stock for the present-day flora of the subcontinent (e.g., Prakash 1979; Bande et al. 1986), with bamboos migrating to the subcontinent in the Tertiary (L. Clark, personal communication). Macrofossils indicate that most plant families and tree taxa that are common today originated and spread under the influence of humid tropical climatic conditions and show a high incidence of porous wood devoid of growth rings (Srivastava and Awasthi 1994). The monsoon phenomenon established to its fullest extent only in the very late Miocene (7–8 M.Y.B.P.), when the Indian landmass collided with the Asian plate and started to raise the Himalayas. As the seasonal monsoon became established, many strictly tropical taxa retreated to moist pockets or became locally extinct, and deciduous taxa reflecting seasonal climates prospered (Whytie 1968; Meher-Homji 1994). Even then, however, fossilized wood of many tropical tree families showed that many relatives of extant Dipterocarpaceae and Elaeocarpaceae became extinct from central and north India after the subcontinent collided with Asia, indicating that nondeciduous vegetation was widespread after bamboos had undergone evolutionary radiations and was widespread well into the orogeny of the still-young Himalayas (Antal et al. 1994). It is hard to imagine conditions that would make fire common in humid, premonsoon tropical forests, and natural fires in later monsoon forests are, and probably were, extremely rare due to lack of ignition.

Seven to eight million years is a potentially long time for selection to act, and it is of course possible that fires occurred before people set them in regions where bamboos were diverse and common, albeit already well diversified. Such a scenario requires much later evolution of monocarpic life histories than is thought by students of the taxa (L. Clark, personal communication), but no one was there to document it. What is known is that in the Quaternary (1.6 M.Y.B.P.), long after bamboos had undergone spectacular evolutionary radiations, increases in the abundance of fossil herbaceous C_4 grasses suggest increasing aridity (Caratini et al. 1991) and quite likely anthropogenic influence. This is instantaneously recent on the geological time scale and the consensus scale of bamboo evolution. If fire could explain bamboo natural history, it would be a recent phenomenon, it would have to explain synchrony and monocarpy over most of the globe (where bamboos still occupy humid equatorial climates), and it would ideally explain the bamboo life cycle in places like India, where 97% of the species show monocarpy and at least rough masting synchrony (eight species are highly synchronous).

Life-History Issues

Monocarpy is strongly favored in expanding populations or in other situations in which the probability of adult survival is low and the probability of successful reproduction high (Cole 1954; Charnov and Schaffer 1973). Particular reasons for ubiquitous deviations from the rule vary, but the general case is that when the fertility at age i is an extreme convex function of reproductive effort at that age, monocarpy is the optimal life history (Gadgil and Prasad 1984). Although they are grasses, woody bamboos are as tall as trees and compete effectively with them. In the Tropics, they occupy open spaces created by their own deaths much like another monocarpic tree of the Neotropics, the canopy rain forest emergent legume *Tachigalia versicolor* (Foster 1977) that acts like a massive vertical bamboo clone in casting dense shade over a wide area, dying, and inundating the ground underneath and the entire vicinity with large, quickly germinating seeds. Vegetative reproduction enables bamboos to spread vigorously during wet months and contributes to their unusual success in habitats disturbed by blowdowns, shifting cultivation, hurricanes, and landslides. In less disturbed situations, however, successful seedling establishment occurs in large gaps created by the death of adult clones. Like *Tachigalia*, death of very large individuals (clones in the case of bamboos) after flowering is itself the large-scale disturbance required to open habitats for vast numbers of seeds and seedlings.

Here we differ with Keeley and Bond (1999) on monocarpy. These authors feel a life cycle is a "metaphor" for a year in either Cole's (1954) result or Charnov and Schaffer's (1973) revision. A more straightforward explanation is Foster's (1977) interpretation that the *Tachigalia* tree (or bamboo clone) need only live long enough to grow large enough to ensure a major disturbance, or gap, upon death. Even if large gaps created by bamboo mortality are inviting to other pioneer species, the prolific bamboo seeding ensures successful bamboo recruitment into the site of the parental clone and in neighboring vacant sites (Stern et al. 1999). Monocarpy in plants is favored under predictable disturbance regimes (Silvertown 1996), and monocarpy with delayed reproduction occurs in woody bamboos, more than half of which belong to closed-canopy tropical forests (Troup 1921; Judzeiwicz et al. 1999) where fire is not a predictable disturbance. Far from requiring fire, profuse inundation of the stand and forest with rapidly germinating substantial seeds provides the mechanism for excluding other species; the dying parent provides the predictable disturbance at an opportune time.

How does one explain synchrony? As in other plants, in rain forest *Tachigalia* or bamboos, synchrony should provide the maximum opportunity for pollination success by wind or animals and for satiation of seed predators (Augspurger 1980, 1981). Long intervals between flowering and fruiting events could further be favored by the requirement not only to occupy space sufficient to ensure a major disturbance upon death but also to satiate seed predators that would otherwise devastate the crops (Janzen 1976; Kelly 1994; also see Augspurger 1981). This explanation was discounted by Keeley and Bond (1999), but the most comprehensive field study of masting to date in lowland Southeast Asia has recently found that isolated asynchronous individual dipterocarps, or seeds planted experimentally, produce essentially no seedling recruits in nonmast years, while all of the effective recruitment occurs during years in which many species produce large mast crops (Curran and Leighton 2000; Curran and Webb 2000). These are perennial species that produce synchronous fruit crops at intervals of several years, but they do it in vast wet forests devoid of natural wildfire. Certainly there is no requirement for fruiting synchrony to be calibrated by fire.

Could fire help? Keeley and Bond (1999) argue that dead bamboo clones would "attract" lightning strikes, much like tall trees, that would provide the ignition required to burn bamboo litter and coincidently incinerate neighboring vegetation. This would ensure occupation of the dying clone by its offspring and favor the spread of bamboos to sites of incinerated neighbors. Lacking evidence of lightning fires and knowing the success of bamboos and other large monocarpic or masting rain forest trees in the absence of fire (e.g., Foster 1977; Curran and Leighton 2000), we doubt the scenario.

To be sure, the evidence of fire effects on bamboo recruitment is poor. None of the papers cited by Keeley and Bond (1999, p. 385) to support the wildfire hypothesis in Indian monsoon forests provides actual evidence of lightning-initiated fire, and most do not mention fire or lightning at all. None makes the argument that central and northeastern Indian forests (where many bamboos evolved) are inherently prone to wildfire caused by other than human activity. We know of no other references that convincingly make the case, based on quantitative evidence or even persuasive anecdotes, that fire helps bamboos of rain forests or monsoon forests recruit. In contrast to fire-resistant seeds of woody plants in fire-prone habitats (Naveh 1975; Keeley and Bond 1997), seeds of some common trees (*Boswellia glabra* and *Lannea coromandalica*) and bamboos in Indian forests are killed by fire (S. Saha, personal observation; also see Marod et al. 1999 for Thailand). If evidence exists that stands of dried bamboo stalks after flowering and seeding are targets of lightning strikes, with the result that bamboo seedlings have a better chance of recruiting than in unburned forests, none is given and none is cited.

Finally, could fire favor synchrony of flowering and fruiting in bamboos of humid tropical forests or monsoon forests, where most masting, monocarpic bamboos occur? If cyclical weather patterns are necessary to provide cycles of lightning strikes, there is no evidence of them. If an occasional "once in centuries" natural fire somehow helped bamboos recruit and "set" a cycle, we do not see how the mechanism would help recruitment over and above the usual rhythm of seed inundation of dying clones, or how killing a large proportion of bamboo seeds and seedlings by fire would help prevent invasion by other species. Nor is it obvious why a rare natural fire would set bamboos on 10-, 20-, or 100-yr cycles and other trees of the same forests on so many other cycles. In no case do we find the arguments more convincing than those of predator satiation (Janzen 1976; Curran and Leighton 2000). In a world of multiple causation, fire might play some role somewhere. In a science in which Occam's razor is valued, an implausible and to date unmeasured set of phenomena and consequences seems superfluous.

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