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BAMBUSOIDEAE

En. Bamboo; Fr. Bambou; Ge. Bambus; Sp. Bambú

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Of the seven grass (Gramineae, Poaceae) subfamilies, bamboo (Bambusoideae) is the most distinctive.[6] Members of this subfamily range from small herbaceous, perennial, tropical humid forest broad-leaved grasses (e.g., *Sucrea*[7,8]) to enormous perennial woody bamboos with stems (culms) to 30 m in height (e.g., *Dendrocalamus, Phyllostachys*[4,6]). One of these large plants may occupy several hundred square meters with a nearly impenetrable thicket of stems. The small forest grass bamboos are of great interest in understanding the evolution of bamboos as they are thought to represent the ancestral types,[8] but have unexceptional flowering behavior in that they flower annually as do most nonbambusoid grasses. On the other hand, the large bamboos have long attracted both curiosity and economic concern because of their peculiar behavior of flowering and then dying synchronously at long supra-annual intervals.[4]

A generalized flowering cycle for one of the 500 to 600 species of large bamboos starts with the germination of a large, even-aged monospecific cohort of seed on terrain occupied immediately previously by the now-dead parents of the cohort. The area may be as large as thousands of hectares and occupy a natural terrain unit such as a valley bottom or hillside, or the cohort may be large clumps scattered through other woody vegetation. There is no seed dormancy. The seedlings grow vegetatively for a species-specific period as short as 7 years and up to as long as 120 years (though the majority grow between 10 and 35 years). During this period most die and a few become extremely large individuals with thousands of long-lived culms and rhizomes. At a species-specific time during the annual seasonal cycle the first members of the cohort begin to flower, and within a year or so better than 95% (usually all) of the members of the cohort have flowered. The cues for within-year timing are unknown, but are undoubtedly the same as those used by any other plant. Synchronous with flowering, the plants shed their leaves; they produce no new culms, other than flowering ones, during the previous 1 to 2 years. As the seeds mature over the following few months the entire vegetative plant dies, probably in large part through exhaustion of its food reserves and mobilization of all available materials for seed filling. If the climate has a marked dry season, the dead stems of the adults often burn on or shortly after the seeds fall, further clearing the soil for vegetative development of the next cohort. If there is a cohort of the same species of bamboo in a neighboring area it is commonplace for it to be on a cycle with the same interfloral period, but out of phase with the other cohort. A country as large as India may contain (or may have contained) many hundreds of cohorts of a given species of bamboo. Occasionally, several conspecific cohorts out of phase with each other occupy the same piece of terrain. Several species of bamboo may occupy the same habitat but have quite different interfloral periods (as well as flower in different parts of the seasonal cycle). The flowers of bamboo are, themselves, not exceptional grass flowers, except that a bamboo culm may bear tens of thousands of flowers (which are usually monoecious).

Plants with a life cycle like that described above range from mid-latitudes and the high-elevation tropics to the subtropics, and from rainforests to extremely seasonal tropical deciduous forests. They are conspicuously missing from almost all of the area within about 5 to 10° of the equator (the conspicuous African exception, *Oxytenanthera abyssinica*, is not only a plant of higher elevations but is also notorious for poorly developed flowering synchrony).

The large bamboos with long interfloral periods appear to be obligatorily outcrossed and wind-pollinated, but closer examination may well encounter more cases of pollination by insects.[1] It is easy to imagine that the synchrony of flowering within the cohort evolved through its value to an outcrossed wind-pollinated plant (individuals that flowered out of phase in an area occupied by only one cohort would be eliminated from the population in one generation). However, this does not explain why the bamboos wait so long between flowering episodes when other large woody plants wait 0 to 10 years at best between wind-pollinated flowering (and seeding).[2,3] To understand the long interfloral period of bamboos we must first briefly discuss the seed biology of bamboos, then a return to the mechanism for a long interfloral period is appropriate.

To condense a lengthy essay on the topic,[4] it appears that the adaptation of a long period between seed production episodes by a bamboo cohort is driven by predation by animals of the highly edible seeds. Since the function of flowering is the maternal or paternal production of seeds, it follows that it is the interrelation with animals that generates the flowering pattern. Bamboos appear to have evolved the following mechanism for escape from seed predators through satiating them (rather than generating a smaller number of toxic or otherwise well-protected seeds). The individual plant stores reserves for flower and seed production for a long time. It then flowers and fruits (seeds) in synchrony with all the other members in the habitat (so-called "gregariously flowering", which is a highly inappropriate term since the bamboo does not flower because it perceives that others are flowering). The number of flowers and seeds that appear in the habitat occupied by the cohort is greater than can be eaten by all the resident, newborn, and migrant animals (if the cohort is to survive). Satiation of these animals requires a very large amount of seed because their numbers can be considerable. This is because bamboo seeds are hardly more than large rice/wheat grains and therefore edible to just about any herbivore. Major bamboo seed predators familiar to most readers are jungle fowl (chickens), forest pigs (pigs of commerce), rats (rodents of all sizes, including *Rattus rattus*), and humans.

There is no way that an individual bamboo plant can extract a reliable cue for flowering at regular many-year intervals from the environment (especially if it has to be a cue very reliably perceived by the other members of the plant population). Instead, all the evidence (mostly circumstantial, but some experimental[4,5]) suggests that the bamboo is genetically programmed to count a certain number of years from its year of germination and then initiate flowering. Such a mechanism is unambiguously one whereby the mutants will be pruned out of the cohort each generation, as will individuals whose internal calendar is insufficiently shielded from environmental effects as to have its flowering (and hence seeding) time advanced or retarded by burning, browsing, cutting, starving, shading, fertilizing, etc. It is very impressive to see a stunted and maltreated 1-m tall 30-year-old bamboo flower in the same year as its unmolested 20-m tall sib a few meters away (small plants effectively act solely as males, large plants act as males and females). On the other hand, removal of the seed predators through habitat destruction or hunting, and introduction of bamboo to other habitats, should favor mutants or poorly shielded individuals whose flowering cycles are marginally out of phase, resulting in eventual loss of intracohort synchrony. For example, the Taiwanese have deliberately introduced conspecifics from different cohorts to their seed-predator-free island and favored out-of-phase mutants; bamboo can be found in flower in Taiwan in any year.

Nothing is known of the biochemical mechanism for counting accurately for so many years. Whatever it is, in addition to being well shielded from the environment it resides in all parts of the plant that can be transplanted. It continues to count accurately even if the plant is moved to quite different parts of the world. However, the author suspects that just as wild bamboos with long supra-annual synchronized within-cohort flowering do not occur much in the deep lowland tropics, introduction of bamboos from the subtropics to the equatorial regions may well result in disrupted counting.

Since bamboo species originally occupied many climate and habitat types and confronted many different levels of intensity of seed predation selecting for intra-cohort synchrony, they will use different cues for flowering within the annual cycle, use different seasonal events to count years, and possess different levels of sensitivity to perturbations of the counting of years. Thus, it may be that if a Japanese species from good volcanic soils is impervious to fertilization as a way of disrupting the calendar, an Indian species from severely impoverished tropical latosols may be susceptible to excessive fertilization. It is impossible to discuss the flowering of bamboos without likewise discussing their seed biology. The connection is even more than just in the timing; the same animals that eat the seeds also eat bamboo flowers and seedlings.[4] This is generally not the case for the synchronously flowering trees that do not die after flowering (e.g., beech, oak, hickory, pine, spruce, dipterocarps, etc.) and that flower and fruit synchronously at shorter intervals. Incidentally, the long interfloral (or intermast) period of these trees is probably an evolved mechanism for escaping seed predation by animals, just as in the bamboos.[2,3]

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