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REVIEW

FLOWERING IN BAMBOO: AN ENIGMA!

S. M. S. D. Ramanayake
Plant Biotechnology Project, Institute of Fundamental Studies, Hantana Road, Kandy, Sri Lanka.
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…when the roots and culms are about to rot,
blossoms and seeds then appear.
They are certain to die when sixty…
Dai Kai Zhi (467 AD)

ABSTRACT

The switch to flowering is the most important event in the life cycle of a plant, signaling its commitment to set seed ensuring survival of the species. Effective and efficient pollination leading to seed set requires that all individuals in a population flower together. Environmental cues are the most effective in bringing about simultaneous flowering in populations growing over wide extents of land.

However, flowering in certain species of bamboo is intriguing, in that the cues that trigger flowering still remain a mystery. These manifest a cyclic pattern of flowering after long, and sometimes regular, vegetative periods that extend up to even 120 years. All individuals growing over vast expanses of land flower in synchrony along with individuals growing elsewhere far away. This phenomenon of mast flowering or mast seeding is the synchronized flowering and production of seed at long intervals by a large population. In bamboo, the population produces wind-pollinated flowers, sets seed in large quantity and perishes. The seeds regenerate to repeat the life cycle. Thus flowering is related to its life span, similar to that of annuals or ephemerals that flower and set seed only once before perishing. Mast flowering is uncommon in the plant kingdom and even in bamboo, only a few species exhibit this phenomenon. The unpredictable nature of this event has brought about devastations to people whose livelihood depends on bamboo. The growing economic importance of bamboo thus requires the understanding of flowering in this group of plants. Induction of flowering *in vitro* would be an approach to this solution in the absence of any other mechanism that can be used to trigger flowering in nature.

Key words: Bamboo, Flowering in bamboo, mast flowering, gregarious flowering, sporadic flowering.

INTRODUCTION

The switch to flowering is the most important event in the life cycle of a plant, signaling its commitment to set seed ensuring survival of the species. Effective and efficient pollination leading to seed set requires that all individuals in a population flower together. How is this achieved? Since early this century it has been experimentally demonstrated that flowering in plants can be triggered by environmental cues (Garner and Allard, 1920, Thomas and Vince-Prue, 1997). Changes in the photoperiod (long or short days), temperature, light quality, vernalization, nutrient deprivation, release from stress, etc are effective in bringing about simultaneous flowering in populations growing over wide extents of land. Thus the reproductive success of a plant depends on its flowering time being adapted to the environment in which it grows. Once the cues that bring about flowering are known, species of economic importance could be stimulated to flower or introduced into new environments conducive to flowering for seed set and thereby agricultural expansion.

In certain species of bamboo, factors that trigger flowering remain a botanical enigma and there is no scientific method yet developed for predicting flowering. These species suddenly flower gregariously and die at the end of it (Janzen, 1976). Death in large populations is a cause of concern due to ecological, social and economic crises that set forth (John and Nadgauda, 2002).

Author's e-mail: shantha@ifs.ac.lk

Bamboo belongs to the sub-family Bambusoideae of the grass family-Poaceae. These comprise the herbaceous and the woody bamboos. Woody bamboos that belong to the tribe Bambusoidae, have played an integral role in the social, cultural and economic development in Asia, throughout history (INBAR, 1999). Bamboo contributes to the livelihood of the rural poor in these countries. Its industrial use in the manufacture of paper pulp dates back to over 2000 years while the use of bamboo strips for writing, dates back to the Han dynasty of China (206 BC – 220AD) (Farrelli, 1938; Marden, 1980). In the recent past a number of bamboo based wood substitutes has been developed (Farrelli, 1938; Jayanetti and Follet, 1998; Cruzet, 2004; Rao *et al*., 2004; Vasudev, 2004). At present this natural resource is overexploited and diminished requiring large-scale replanting (Dransfeild and Widjaja, 1995). Rare seeding in bamboo requires propagation by vegetative methods. Conventional methods of vegetative propagation cannot cater to the present scale of demand for propagules and the alternative is the use of tissue culture techniques. This is now applied in commercial propagation of a few bamboo species (Shirgurka *et al.*, 1996; Arya *et al.*, 1999; Ramanayake *et al.*, 2006). Selection of propagules for plantation establishment and management of plantations would require understanding the causes that trigger gregarious flowering in bamboo.

Flowering in bamboo

In bamboo, the duration of the vegetative phase and switch to flowering varies according to the species. In some species such as *Bambusa vulgaris*, the vegetative phase is persistent. This species flower sporadically when only a few plants flower but set no seed (Ramanayake and Yakandawala, 1995; Koshy, 1997). McClure (1966) reported that although the species has never been “rejuvenated” by sexual reproduction, it is one of the most vigorous of the bamboos. In contrast, there are other species with a persistent tendency to flower but set no seed. *Bambusa atra* and *Schizostachyum brachycladum* (introduced to Sri Lanka from Indonesia) constantly flower but with no seed set and continue to grow vigorously year after year. There are yet others such as the endemic species, *Ochlandra stridula* (bata) that flower and set seed annually.

The species that are the most intriguing are those that fall between a state of constant sterility and constant flowering to manifest a cyclic pattern of flowering after long periods of vegetative growth that last even up to 120 years. All individuals growing over vast expanses of land flower in synchrony along with individuals growing elsewhere even far away. A recent example is the gregarious flowering of a temperate bamboo, *Fargesia murielae*, which was introduced to Europe and the US from China in the early 1800’s (Palen, 2006; Oprins and Trier, 2006). The species flowered and set seed during the 1990’s throughout Europe, US and China although environmental conditions, pests and disease incidences and various other factors that the plants were exposed to varied. The phenomenon, also termed mast flowering or mast seeding, is the synchronized flowering or production of seed at long intervals by a population of plants. Synchronized mast seeding in iteroparous plants such as oaks, beeches, conifers and dipterocarps is triggered by environmental cues (Janzen, 1974 and 1976; Koening and Knops1998). But bamboo is semelparous or monocarpic. The population produces wind-pollinated flowers, sets seed in large quantity and perishes. Death is attributed to reproductive exhaustion caused by the movement of food reserves from the vegetative parts. If however, the rhizome is left with sufficient resources, the clump is able to recover although all aerial culms that flower die. The seeds germinate with the first rains and this new generation repeats the life cycle. The thalipot palm (*Corypha umbraculifera*) also shows some semblance of gregarious flowering (Petch, 1925). But in this species death is a consequence of cessation of growth due to the transition of the apical meristem into a massive inflorescence followed by seeding.

Sometimes during gregarious flowering in bamboo, a few clumps may remain in a state of vegetative growth for no known reason. At the same time these species may also show sporadic flowering in some clumps within populations during the intermast period and also set seeds. Goraya *et al.*, (2003) reported that although *Arundinaria falcata* is a gregariously flowering species, it also flowers sporadically every year. Rao (1998) observed that sporadic flowering is very regular in certain areas. In Kanchanaburi area of Thailand many species of bamboo in the bambusetum and the nearby forests, flower sporadically. Clump after clump in a population takes turn to flower and seeds are collected once or twice a year. It is becoming increasingly clear that sporadic flowering is very common in many species as observed in different countries (Rao, 1998). It is not known what triggers a few clumps to set flower in this manner.

Although environmental factors influence the growth of plants, and in the majority of plants they trigger flowering, factors that trigger flowering in bamboo still remain a mystery. It is not possible to observe the cyclic nature of flowering due to their long life spans necessitating dependence on past records of flowering. Many causes have been attributed to trigger gregarious flowering in bamboo but it has not been possible to establish their consistency. Drought has been thought to trigger mast flowering. Seifriz (1950) points out that although these two phenomena, when they occur together are noticed, the appearance of one without the other is rarely noticed. His studies on flowering of *Chusquea*, a new world bamboo in the mountains of Jamaica, showed that gregarious flowering occurred in times of drought as well as when there was no drought, and there also have been years of drought without flowering. If bamboo flowering is affected by environmental or climatic factors, it only requires climatic tracking for verification.

Depletion of nutrients is another cause attributed to trigger bamboo flowering, but again there is no evidence to support this. A clump does not develop any new vegetative culms in the few years before and during flowering. During flowering, there is a switching of resources from vegetative to reproductive parts when stored nutrients are used up in the production of vast quantities of flowers and seeds.

According to Janzen (1976) who studied natural stands of bamboo and their records of past flowering, there are at least 137 Indian-Asian species that have populations that flower and set seed synchronously at regular and supra-annual intervals. He suggested the presence of an internal mechanism of a biological clock that controls flowering in bamboo. In fact, the life cycle of bamboo is similar to that of annuals or ephemerals that flower and set seed only once before perishing. But unlike annuals and ephemerals, bamboos attain tree-like proportions during a long period of vegetative growth before flowering and dying. Thus the monocarpic flowering habit of the herbaceous grasses has persisted as a surviving evolutionary trace in these woody forms (Rao, 1998). Mast flowering is uncommon in the plant kingdom and even in bamboo, only a few species exhibit this phenomenon.

Yet another factor under speculation is that an unknown rhythmic climatic cycle of long duration may be the causal factor like in boreal coniferous trees, beech, oak and dipterocarps that manifest mast seeding (Janzen, 1974 and 1976; Koening and Knops, 1998). If this is so, all bamboo species that flower gregariously must respond together. This has not been observed. In bamboo forests of Mizoram, India, two gregariously flowering species, *Melocanna baccifera* and *Bambusa tulda* occur together. Both are reported to flower every 48 years but not at the same time. *B. tulda* flowers 18 years after *M. baccifera*. According to Indian forest records *B. tulda* gregariously flowered in 1880 through 1884 and in 1928 through 1929. Mohan Ram and Hari Gopal (1981) had observed flowering in this species in 1976 when gregarious flowering lasted until 1979. They reported that gregarious flowering was first observed in the southern parts of Mizoram, spread to the northern parts and progressed to the Assam plains. They also studied gregarious flowering in *M. bambusoides* (*M. baccifera*) and according to Indian forest records, this has taken place in 1910-1912 and 1958-1959 in northern India. It flowered in synchrony in Chitagong at the same periods (Janzen, 1976). The species is expected to flower in 2007, as it is believed to have an intermast period of 48 years (Tripathi *et al.*, 2002). This expectation has been realized as the species has started to flower gregariously in northeastern India in about 1.7 million ha (Sethi, 2004). Interestingly, *M. baccifera* (introduced to Sri Lanka from India in 1910), in the Royal Botanic Gardens (RBG), Peradeniya is also flowering in synchrony (Ramanayake and Weerawardene, 2003).

Dendrocalamus strictus is another bamboo that flowers gregariously in Indian bamboo forests. It is the most widely distributed species in India and used extensively in paper pulp manufacture. In this species there are cohorts that have different intermast periods of 25 years in South India, 40 to 45 years in North East and Central India, 45 years in Bangladesh and 65 years in West India (Banik, 1994). The species also flowers sporadically and seeds are available annually.

Arundinaria falcata and *A. spathiflora* are two montane bamboos in the Western Himalayan State of Himachal Pradesh, of great ecological and social significance. *A falcata* shows an intermast period of 28 to 30 years (Goraya *et al.*, 2003; Vaitham and Chandra, 2003). They flowered gregariously across the state in 2000 and 2001, respectively. Some clumps remained in a vegetative condition during this time, whereas one or other odd clumps flower sporadically almost every year during the intermast period. *A. falcata* produced abundant seed resulting in profuse regeneration during gregarious flowering. This species is reported to have a 28 to 30 year cycle. Information about flowering in *A. spathiflora* is limited. However, it is said to have a 60-year cycle of gregarious flowering while a few instances of sporadic flowering is also reported (Goraya *et al.*, 2003).

Pseudoxytenanthera ritcheyi (Munro) Naithani flowered gregariously in Western Ghats in 1999 (Bhangre, 2001). Kulkarni *et al.* (2001) also reported that this species flowered gregariously at the same time in Pune, Maharashtra.

Bamboos of the New World too, have species that exhibit mast flowering. Seifriz (1950) observed mast flowering and seeding of *Chusquea abeitifolia* in Jamaica. His studies indicated an intermast period of 32 years in this species. Records showed that it flowered in 1880 through 1886 in the mountains of Jamaica. A living specimen from Jamaica planted in the Kew gardens in the early 1880 also flowered at the same time. Seifriz (1950) in his visit to Jamaica in 1919, observed the species only as an entangled dead mat of plants together with a foot-high seedlings, covering the mountains. Thus the offspring was successfully replacing the parents and these flowered in 1948- 1949 repeating the 32-year life cycle.

Gregarious flowering is observed in bamboos under cultivation as well as in the wild. This is contrary to Janzen’s (1976) belief that mast flowering and seeding occurred only in wild stands of bamboo. According to Seifriz (1950) gregarious flowering is due to gregarious planting either by nature or man. The industrial utilization of bamboo has led to the replanting of bamboo on a large scale. Large-scale planting will require clonally raised propagules due to scarcity of seeds. To prevent occurrence of gregarious flowering in plantations, precautionary measures such as ensuring a wide genetic base and good management practices are necessary. However, in the absence of any reliable methods to prevent flowering in bamboo, it is essential to understand the flowering behaviour and the genetic mechanisms involved.

Facts and Myths about bamboo flowering

Flowering in bamboo is believed to be an ill omen, leading to famine, death and natural disasters in cultures associated with bamboo (Mohan Ram and Hari Gopal, 1981; John and Nadgauda, 2002). Factually, when bamboo flowers gregariously, it leads to economic, social and ecological havoc. During gregarious flowering, large quantities of seeds, sometimes a layer foot or so high, are formed on the ground. Rodents and many other animals relish this nutritious source of food and reproduce fast to increase in number. People in these areas too gather the seeds for consumption (Janzen, 1976). Once the seeds are exhausted due to their germination, the rats turn to devour crops in the vicinity causing famine. In northeastern India, flowering in *B. tulda* (Mizo name *Rawthing*) is associated with the ‘Thingtam’ famine and devastation. ‘Mautam’ famine is associated with *M. baccifera* (Mizo name *Mautak*). ‘Mautam’ famine is said to be more severe as this species bear large fruits and can thus support a larger rat population. These famines have occurred in years associated with the gregarious flowering. Once the bamboo dies after flowering, the people whose livelihood depended on the bamboo resource are severely affected. The dead culms are a fire hazard. The land becomes bare as it takes time for the new generation to establish. Bare land could be disastrous in mountainous areas leading to landslides. In the late 1950s when *M. baccifera* in Mezoram flowered gregariously, the people formed the ‘Mizo National Famine Front’, when the Government failed to respond soon enough to assist their suffering. Their disillusionment and anger finally resulted in the formation of an ethnic political party that led to a 20-year war ending with a peace accord in 1987. At present, *M. baccifera* has commenced to flower and is expected to spread over a larger extent of land. The impending gregarious flowering in this species, triggered the Government of India to plan ahead in order to combat the recurrence of suffering experienced during the past (Trivedi *et al.*, 2002). Strategies to utilize the resource in the paper pulp industry, keep close watch on the rodent population, mapping of non- flowering cohorts, fast regeneration of bamboo forest after flowering, provision of food relief and medical supplies to affected human populations, are some of the plans that are underway (Sethi, 2004; Katwal and Pal, 2004). However, most of the forest areas in Northern India are inaccessible. This indicates a measure of the problem created by incidence of mast flowering in bamboo forests.

A fairly recent episode of bamboo flowering in Thailand caused a heavy loss in the bamboo shoot processing industry. *Dendrocalamus asper*, used for harvesting edible shoots, flowered gregariously in 1994 and set seed in 1995 in an area of 40,000 ha. The total annual loss is reported to be US $ 80 million (Tammincha, 1995). It is reported that the species was introduced to Thailand from China about 80 years ago and the planting area rapidly increased with the development of the shoot processing industry. Gregarious flowering was unexpected. This species is also found in Sri Lanka but has not been reported to flower.

In China, bamboo flowering is notably associated with the giant panda bear (*Ailuropoda melanoleuca*) (Taylor and Zisheng, 1997). Pandas are obligate bamboo browsers and thus have very specific eating habits. They feed on shoots of the bamboo species *Bashania* and *Fargesia*. Flowering in these species cause deprivation of food for the Pandas. In the past when gregarious flowering occurred, pandas were able to move to other locations where non-flowering cohorts were growing. However, with the recent agricultural expansions, the land has become fragmented and the pandas are now unable to move to locations of non-flowering bamboo stands as they did in the past. Thus the panda bear population has become endangered mainly due to habitat destruction rather than to bamboo flowering.

Gregarious flowering in another group of plants

Another group of plants known to exhibit mast flowering followed by death include some woody shrubs of *Strobilanthus*. E.g. *S. ixiocephalus*, *S. callosus*, *S. kunthianus* etc. of the family Acanthaceae (Santapau, 1962). *S. kunthianus* of the Nilgiri hills of India, which because of its profuse blue flowers has given the name to the hills, is said to flower every 12 years. Santapau (1962) described that during mast flowering extensive areas are covered with blue, pleasantly scented flowers. Species of *Strobilanthus* in Sri Lanka are collectively known as Nilu or Nelu. Their flowering is reported to attract attention not only because of the unusual sight of a large number of plants massed together in flower, but also because of the many jungle fowl that gather to feed on the seed after flowering, an easy prey for the local sportsman (Petch, 1925). Twenty-eight species of *Strobilanthus* are reported in Sri Lanka and there are probably more growing in the upcountry or low country forests. Petch (1925) reported that information concerning flowering of Nilu in Sri Lanka was derived principally from Mr T. Farr, a sportsman and a naturalist who resided up country and had made observations on this subject. *Strobilanthus sexennis* is the commonest and the largest Nilu of the hill forests and becomes a small tree up to 12 feet high with a stem 4 to 5 inches in diameter. According to records of flowering periods kept by Mr Farr, it has an 11 or 12-year intermast period. When this species flowers, the general Nilu flowering becomes noticeable and when it dies in consequence of flowering, the dead stems, covering areas extending for miles, are an equally conspicuous feature of the landscape. The smaller species, *S. pulcherimus*, *S. calysinus*, *S. anceps* and others flower at the same time on the same areas. It is also possible that they flower and die at other times but remain unnoticed as they are more or less hidden from view. In 2001, we as Sri Lankans were fortunate to observe gregarious flowering of a species we suspect to be *Strobilanthus sexennis* in the Horton Plains. The shrubby plants of this species on either side of the road were all in bloom with blue flowers. Investigations on flowering in species of *Strobilanthus* and other members of the Family Acanthaceae in Sri Lanka are lacking after those made by Mr Farr and recorded by Petch (1925). The best examples of gregarious flowering in Sri Lanka are afforded by species in this family. It is unfortunate that Nilu is not that abundant at present in Sri Lanka, due to clearing of forestland. Nevertheless, investigations on flowering, even in the remaining populations are necessary, as they will contribute to understanding this peculiar phenomenon of semelparous mast flowering limited to only a few groups of plants.

Aechmanthera gossypina (Nees) is another species of the family Acanthaceae that flowers gregariously in India. Garbayal (2000) reported that the species flowered gregariously in Chaudan valley of Kumaon hills of the Uttar Pradesh in 1999. It has a 12-year flowering cycle and produces violet –blue flowers and set seed before dying. This species is neither grazed by animals nor of any commercial value to the local people, but has some cultural significance. The inhabitants of the valley believe it to be a symbol of evil and destroy it ceremoniously every 12 years to symbolize victory over evil! A scientifically interesting fact is that once the seeds germinate the plant is not seen for the next two years as it grows underground and thereafter every year, the main stem elongates producing a node each year. Once 10 nodes have developed after 10 years of growth above ground, flowering occurs gregariously in the population. Thus like in bamboo, flowering in *A. gossypina* is related to age. Once the plant has reached a developmental stage related to age it becomes competent to flower. This has not been studied or reported in bamboo, possibly because of practical problems associated with monitoring vegetative growth of the massive underground and above ground parts over the many years before flowering.

***In vitro* flowering in bamboo**

This is the development of inflorescences in axillary shoots of bamboo in tissue culture. Induction of *in vitro* flowering in bamboo was first reported by Nadgauda *et al*. (1990). They reported that in *D. strictus, D. brandisii* and *B. arundinacea* (*B. bambos*) axillary shoot cultures developed viable spikelets and also produced fertile seeds in the presence of coconut water and growth regulators. Since the axillary shoots were initiated in juvenile shoots from germinated seeds, it was considered to be an expression of precocious flowering. Subsequently many others reported *in vitro* flowering in other species such as *D. hamiltonii* (Chambers *et al.,* 1991), *D. giganteus* (Rajapakse, 1992) in juvenile axillary shoot cultures. Somatic embryos have also given rise to *in vitro* flowering in *B. vulgaris*, *D. giganteus*, *D. strictus* (Rout and Das, 1994). Later, *in vitro* flowering in axillary shoot cultures initiated from field culms in *D. giganteus* (Ramanayake *et al.*, 2001a) and *B. edulis* (Lin *et al*., 2004) was also reported. Presence of cytokinins and stress has been attributed for flowering *in vitro* (Geilis *et al.*, 1997; Ramanayake *et al.*, 2001a). Reversion of flowering has also been observed under *in vitro* conditions. Contribution of stress and stress release in induction of *in vitro* flowering and its reversion respectively, are discussed in Ramanayake *et al.* (2001a). Viability of *in vitro* pollen is low. However, in vitro flowering is inconsistent and in all these reports the causes of flowering are not clearly established. Research to identify factors that bring about consistent flowering need further investigations. Induction of *in vitro* flowering has several other advantages. The molecular events related to flowering could be studied more readily *in vitro* than in the field where flowering cannot be controlled. In nature, different species rarely flower at the same time. But they may be induced to flower in synchrony by *in vitro* techniques and used in wide hybridization for the development of improved varieties (Nadgauda and John, 2004). *In vitro* flowering associated with seed set could be a perennial source of seeds for propagation.

Flowering in bamboo is taxonomically important for identification of species. Since flowering is rare in nature, only vegetative parts are available for identification. These are not always reliable as morphological features could vary with environment. *D. hookeri* is a species that we identified using morphological features in the absence of natural flowering. Now we have been able to induce *in vitro* flowering in axillary shoots of this species and studies to confirm the species identity are possible (Fig, 1 C).

Flowering of bamboo in Sri Lanka

Our observations of flowering in bamboo in Sri Lanka for over a decade have also generated some findings. We observed flowering in the giant bamboo, *D. giganteus* in nature and in tissue cultures (Ramanayake and Yakandawala, 1998; Ramanayake *et al*., 2001a, b) (Fig. 2). Although the species is reported to have a life cycle of 75 years by Janzen (1976), our studies did not confirm it. A relatively large number of clumps flowered periodically during this time ruling out sporadic flowering. Since the entire population did not flower, this incidence was not one of gregarious flowering. Seed set was rare (Fig. 1 A & B). Only the flowering culms died and there was subsequent regeneration from the rhizome, except for two clumps, which died. Many of the flowering clumps resumed vegetative growth periodically. *D. giganteus* was introduced to Sri Lanka in 1856 (MacMillan, 1907; Petch, 1925). Our studies as well as reports of past curators of the RBG, showed that some of the plants in the RBG flowered, set seed and did not die at the end of flowering (Macmillan, 1907; Petch, 1925; Ramanayake and Yakandawala, 1998). We were also able to induce flowering *in vitro* in axillary shoots of a 75-year-old clump that did not flower in nature (Ramanayake *et al*., 2001a). Thus if bamboo flowering is caused exclusively by the internal mechanism of a biological clock running in harmony in the field clump and its shoots growing in tissue culture, flowering is expected to occur together in both. Since this did not happen, it indicated that there maybe more than one pathway that lead to flowering in bamboo. However, a clump of *M. baccifera* in the RBG Peradeniya flowered in synchrony with others of the species that commenced gregarious flowering in their native habitat in Northeast India (Ramanayake and Weerawardene, 2003).

A flowering bamboo was considered to be bad luck even in Sri Lanka where bamboo flowering is rare. Flowering of giant bamboo in home gardens was a problem to inhabitants due to the fall of vast quantities of flowers that even polluted water in wells and streams. The dying culms that tended to collapse over houses and electric wires were a hazard.

A few yellow bamboo (*Bambusa vulgaris* var vitata) clumps also flowered sporadically and all individuals that flowered died without regeneration (Ramanayake and Yakandawala, 1995). Flowering of many individuals of the same species recently in India leading to death with no seed set caused a speculation that the species was heading for extinction (Koshy, 1997).

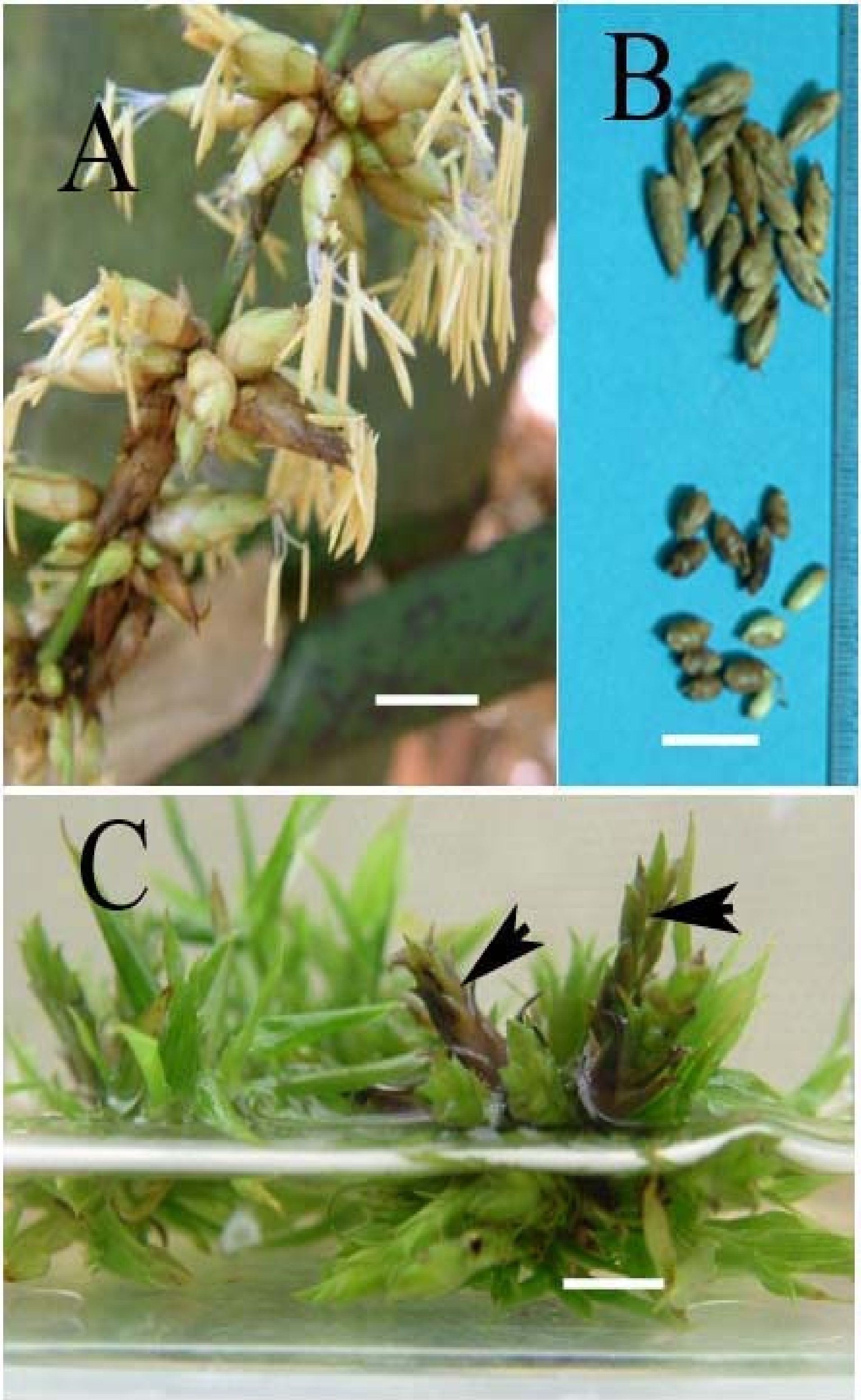

Figure 1. Flowering in *Dendrocalamus giganteus* and *D. hookeri* in nature and in vitro. A. spikelets of *D. giganteus* in a flowering culm in the field, bearing florets at anthesis with anthers exerted. B. Caryopsis (top) and seeds (bottom) of *D. giganteus* after dehusking. C. Spikelets (pointed by arrow) that developed *in vitro* in *D. hookeri.*

Figure 2. A clump of *Dendrocalamus giganteus* in Kandy with dying culms after flowering

Bambusa atra, is a species introduced to Sri Lanka from Indonesia. This is a constantly flowering species and does not die when flowering culminates in the shoots. It also flowered *in vitro* (Ramanayake *et al*., 2001b).

Although *D. asper* has not been observed to flower in Sri Lanka, we were able to induce *in vitro* flowering in axillary shoot cultures raised from seeds obtained from Thailand when the species mast flowered.

Gene expression during flowering

It is now known that the transition to flowering in plants is governed by genes. With the recent development of advanced techniques of tracing of biological events at the molecular level, the molecular mechanism of flowering is being revealed (Weigel and Nilsson, 1995; Ruize-Garcia *et al*., 1997; Pineiro and Coupland, 1998; Somers, 1999). Flowering is accompanied by the transition of the apical meristem from a vegetative to a reproductive mode of growth to develop into a flower or an inflorescence instead of vegetative shoots. A large number of genes associated with flowering are expressed during this transition (Lin, 2000). Perception of environmental cues and the proceeding events that lead to floral development have been extensively studied. A number of pathways that lead to flowering have been discovered (Simpson and Dean, 2002). However, the genetic mechanism of flowering related to age, as in bamboo, is yet to be discovered. The intriguing phenomena of gregarious flowering indicate that it is not brought about by external factors but is defined by an internal mechanism of gene activity. Flowering, when bamboo reaches a certain age, and the regular fixed flowering cycles in certain species, indicate an age-related gene activity. At the same time, it does not imply that environmental factors do not have an influence. Incidences of flowering *in vitro* or damage due to fire or cutting down may also sometimes trigger this internal mechanism by alternate pathways of flowering discovered in many other plants.

During flowering, a bamboo clump remains almost leafless (Fig. 2). It does not produce new culms during flowering or in the year before flowering (Rao, 1998). Thus it would be necessary to study these well in order to understand the causal factors and relationship between vegetative growth and flowering.

Large-scale plantation establishment and prevention of flowering

It is worth understanding the flowering behavior of bamboo especially in large-scale propagation and plantation establishment. At present, Sri Lanka has a very limited bamboo resource both qualitatively and quantitatively. Mast flowering in bamboo does not occur in Sri Lanka possibly due to occurrence of only small populations. Bamboo has a vast economic potential for Sri Lanka. Seifriz (1950) speculated that gregarious flowering could be due to gregarious seeding in nature or planting by man. Therefore, in our quest for expansion of bamboo plantings, it is necessary to be cautious in selecting planting material of known origin and establishing a wide genetic base to alleviate problems of gregarious flowering. Selection of non-flowering cohorts and cohorts that flower out of phase during gregarious flowering and using them in breeding programs are also important.

REFERENCES

Arya, S., Sharma, S., Kaur, R. and Arya, D. (1999). Micropropagation of *Dendrocalamus asper* by shoot proliferation using seeds. *Plant Cell Reports* **18**(10): 879 – 882.

Banik, R. L. (1994). Diversities, reproductive biology and strategies for germplasm conservation of bamboos. In: Ramanatha Rao V. and Rao A. N. eds. *Bamboo and Rattan genetic resources and use. Proceedings of the first INBAR biodiversity, genetic resources and conservation-working group*. 1994. Singapore, Pp. 1 – 22.

Bhangre, A. B. (2001). A note on bamboo flowering. *Indian Forester* **127** (4): 485 – 486.

Chambers, S. M., Heuch, J. H. R. and Pirri, A. (1991). Microprpagation and *in-vitro* flowering of the bamboo *Dendrocalamus hamiltonii* Munro. *Plant Cell Tissue and Organ Culture* **27** (1): 45-48.

Crouzet, S. (2004). Bamboo shoots for the south of France. In: *Abstracts of Proceedings of the VIIth World Bamboo Congress*, New Delhi, India, Feb – March 2004. Pp 27.

Dransfield, S. and Widjaja, E. A. (1995). *Plant resources of South-East Asia No. 7-Bamboos.* Backhuys Publishers, Leiden, Pp.189

Farrelli, D. (1938). *The book of bamboos.* The Sierra Club Books, San Francisco, USA.

Garbayal, S. S. (2000). Gregarious flowering in *Aechmanthera gossypina* (Nees) Nees (Kangadi) in Chaudan valley, Kumaon Hills of Uttar Pradesh. *Indian Forester* **126** (2): 197 – 199.

Garner, W. W. and Allard, H. A. (1920). Effect of the relative length of day and night and other factors of the environment on plant growth and reproduction in plants. *Journal of Agricultural Research* **18**: 553 – 606.

Geilis, J, Goegthebeur, P. and Debergh, P. (1997). Morphological and biochemical aspects in flowering of bamboo – the development of model systems. In: Chapman G. P. (ed) *The Bamboos, Linnean Society Symposium Series (No 19)* Academic Press, London, Pp. 179-186.

Goraya, G. S., Jishta, V., Kapoor, K. S. and Pal, M. (2003). Mast flowering in montane bamboos in Himachal Pradesh: ushering in the new millennium! *Indian Forester* **129** (8): 1013.

INBAR (1999). *Socio-economic issues and constraints in the Bamboo and Rattan sectors: INBAR's assessment*. International Network for Bamboo and Rattan. Working Paper No. 23, Pp. 28.

Janzen, D. H. (1974). Tropical black-water rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* **6**: 69 – 103.

Janzen, D. H. (1976.). Why bamboos wait so long to flower. *Annual Reviews of Ecology and Systematics* **7**: 347 – 391.

Jayanetti, D. L. and Follet, P. R. (1998). *Bamboo in construction; an introduction.* INBAR technical report number 15. TRADA technology, UK and INBAR. South Bucks Press, UK.

John, C. K. and Nadgauda, R. S. (2002). Bamboo flowering and famine. *Current Science* **82** (3): 261 – 262.

Katwal, R. P. S. and Pal, M. (2004). Gregarious flowering in bamboo and strategies for its management in India. In: *Abstracts of Proceedings of the VIIth World Bamboo Congress*, New Delhi, India, Feb – March 2004, Pp. 47.

Koening, W. D. and Knops, M. H. (1998). Scale of mast seeding and tree-ring growth. *Nature* **396**: 225 – 226.

Koshy, C. K. (1997). *Bambusa vulgaris* blooms: a leap towards extinction? *Current Science* **72** (9): 622 – 624.

Kulkarni, D. K., Jagtrap, A. P., Nigam, A. K. and Phale, S. G. (2001). Gregarious flowering of *Pseudoxynanthera ritcheyi* (Munro) Naithani at Rajgad Fort, Pune, Maharashtra. *Indian Forester* **127** (7): 831 – 833.

Lin, C. (2000). Photoreceptors and regulation of flowering time. *Plant Physiology* **123**: 39 – 50.

Lin, C. S., Lin, C. C. and Chang, W. C. (2004). Effect of thidiazuron on vegetative tissue-derived somatic embryogenesis and flowering of bamboo, *Bambusa edulis*. *Plant Cell Tissue and Organ Culture* **76**: 75-82.

Macmillan, H. F. (1907). Flowering of *Dendrocalamus giganteus* the 'Giant bamboo'. *Annals of the Royal Botanic Gardens, Peradeniya* Vol. **IV**: 123 – 129.

Marden, L. (1980). Bamboo the giant grass. *National Georgraphic.* **158**: 502 – 529.

Mc Clure, F. A. (1966). *The Bamboos, a fresh perspective*. Harvard University Press, Cambridge.

Mohan Ram, H. Y. and Hari Gopal, B. (1981). Some observations on the flowering of bamboos in Mizoram. *Current Science* **50** (16): 708 – 710.

Nadgauda, R. S. Parasharami, V. A. Mascarenhas, A. F. (1990). Precocious flowering and seeding behaviour in tissue-cultured bamboos. *Nature* **344**: 335 - 336.

Nadgauda, R. S. and John, C. K. (2004). Bamboo hybridization: hope, despair and promise. In *Abstracts. Proceedings of the VIIth World Bamboo Congress*. New Delhi, India, Feb – March 2004, Pp. 07.

Oprins, J. and Trier, H. V. (2006). *Bamboo – a material for landscape and garden design.* Birkhauser Publishers, Basel, Berlin, Boston. Pp 34 – 35.

Palen, J. V. D. (2006). *Fargesia nitida* flowers! *Newsletter of the Southern California Chapter of the American Bamboo Society* **16** (1): 2 – 5.

Petch, T. (1925) Gregarious flowering. *Annals of the Royal Botanic Gardens, Peradeniya*. Vol **IX**: 101 – 117.

Pineiro, M. and Coupland, G. (1998). The control of flowering time and floral idenetity in *Arabidopsis*. *Plant Physiology* **117**: 1 – 8.

Rajapakse, M. C. (1992) Studies on the *in vitro* development of *Dendrocalamus giganteus*. M. Phil thesis, Postgraduate Institute of Agriculture, University of Peradeniya, Sri Lanka.

Ramanayake, S. M. S. D., and Yakandawala, K. (1995). Some observations in the flowering in *Dendrocalamus giganteus* and *Bambusa vulgaris*. In: H. P. M. Gunasena. *Multipurpose Tree Species in Sri Lanka. Proceedings of the 6th Regional Workshop on Multipurpose Tree Species In Sri Lanka*, August 1995, MPTS Research Network, Faculty of Agriculture, Peradeniya, Sri Lanka, Pp. 116 – 120.

Ramanayake, S. M. S. D. and Yakandawala, K. (1998). Incidence of flowering, death and the phenology of the giant bamboo (*Dendrocalamus giganteus* Wall. Ex Munro). *Annals of Botany* **82** (6): 779 – 785.

Ramanayake, S. M. S. D., Wanniarachchi, W. A. V. R. and Tennakoon, T. M. A. (2001a)**.** Axillary shoot proliferation and *in vitro* flowering in an adult giant bamboo, *Dendrocalamus giganteus* Wall. Ex Munro. In vitro *Cellular and Developmental Biology - Plant* (*Special Issue of the IAPTC&B)* **37**: 667 – 671.

Ramanayake, S. M. S. D., Weerawardene, T. E. and Amarasekera, V. N. (2001b). Micropropagation and *in vitro* flowering in *Bambusa atra*. In: *Abstracts, Proceedings of the Sri Lanka Association for the Advancement of Science*. 56th Annual Session. December 2001, Colombo, Sri Lanka.

Ramanayake, S. M. S. D. and Weerawardene, T. E. (2003). Flowering in a bamboo, *Meloccana baccifera* (Roxburgh) Kurtz ex Scheels (Bambusoideae: Poaceae) *Botanical Journal of the Linnean Society* **143** (3): 287-291.

Ramanayake, S. M. S. D., Meemaduma, V. N. and Weerawardene, T. E. (2006). *In vitro* shoot proliferation and enhancement of rooting for the large-scale propagation of yellow bamboo (*Bambusa vulgaris* 'Striata'). *Scientia Horticulturae* **110**: 109 – 113.

Rao, A. N. (1998). Genetic diversity of woody bamboos- their conservation and improvement. In: Rao A. N. and Rao R. (Eds) *Bamboo conservation, diversity, ecogeography, resource utilization and taxonomy. Proceedings of a workshop* May 1998, Yunnan, China.

Rao, C. B. J., Kumar, K. E. R, Ramachandra, B. and Khoday, S. H. (2004). Bamboo biomass for power generation. In: *Abstracts of Proceedings of the VIIth World Bamboo Congress*, New Delhi, India, Feb – March 2004, Pp. 41.

Rout, G. R. and Das, P. (1994). Somatic embryogenesis and *in vitro* flowering in 3 species of bamboo. *Plant Cell Reports* **18**: 683-686.

Ruiz-Garcia, L., Madueno, F., Wilkinson, M., Haughn, G., Salinas, G. and Martinez-Zapeter, J. M. (1997). Different roles of flowering-time genes in the activation of floral initiation genes in *Arabidopsis*. *The Plant Cell* **9**: 1921 – 1934.

Santapau, H. (1962). Gregarious flowering of *Strobilanthus* and bamboos. *Journal of the Bombay Natural History Society* **59**: 688- 696.

Saxena, S. and Dhawan, V. (1999). Regeneration and large-scale propagation of bamboo (*Dendrocalamus strictus* Nees) through somatic embryogenesis. *Plant Cell Reports* **18** (5): 438 – 443.

Seifriz, W. (1950). Gregarious flowering of *Chusquea*. *Nature* **22**: 635 – 636.

Sethi, K. S. (2004). Flowering of muli bamboo (*Melocanna baccifera*) and its management in Tripura. In: *Abstracts. Proceedings of the World Bamboo Congress* 27th Feb. – 4th March 2004, New Delhi, India. Pp 46.

Shirgurka, M. V., Thengane, S. R., Poonawala, I. S., Jana, M. M., Nadgauda, R. S. and Mascarenhas, A. F. (1996). A simple in vitro method of propagation and rhizome formation in *Dendrocalamus strictus* Nees. *Current Science* **7** (10): 940 – 943.

Simpson, G. G. and Dean C. (2002). *Arabidopsis*, the Rosetta stone of flowering time? *Science* **296**: 285 – 289.

Somers, D. E. (1999). The physiology and molecular bases of the plant circadian clock. *Plant Physiology* **121**: 9 – 20.

Tammincha, S., (1995). Bamboo shoot industry and development in Thailand: the physio-social economic implications. In: *Proceedings of the 1Vth International Bamboo Congress*. 19th – 20th June 1995, Bali, Indonesia.

Thomas, B. and Vince-Prue, D. (1997). *Photoperiodism in plants.* 2nd edition. Academic Press, New York.

Taylor, A. H. and Zhisheng, Q. (1997). The dynamics of temperate bamboo forests and Panda conservation in China In: Chapman G. P. (ed) *The Bamboos*, Linnean Society Symposium Series (No 19) Academic Press, London, Pp. 179-186.

Tripathi, Y. L., Singh, H. P., Pandey, B. K. and Kaushik, P. (2002). Prospects of bamboo flowering and resource management: an industrial perspective In: *Proceedings of Expert Consultation on Strategies for Sustainable utilization of bamboo Resources Subsequent to Gregarious Flowering.* Rainforest Research Institute, Jorhat, Assam, India, 24 – 25th April 2002, Pp. 80 – 91.

Trivedi, S., Pattanaik, S., Pathak, K. C., Khatri, P. K. and Prasad, K. G. (2002). Regeneration strategies following gregarious flowering of bamboo in northeast India. In: *Proceedings of Expert Consultation on Strategies for Sustainable utilization of bamboo Resources Subsequent to Gregarious Flowering.* Rainforest Research Institute, Jorhat, Assam, India, 24 – 25th April 2002, Pp. 98 –102.

Vaitham, H. B. and Chandra, S. (2003). Gregarious flowering of a bamboo (*Drepanostachyum falcatum*) *Indian Forester* **124** (8): 663 – 666.

Vasudev, S. (2004). Market opportunities for bamboo composite in India. In: *Abstracts of Proceedings of the VIIth World Bamboo Congress*, New Delhi, India, Feb – March 2004, Pp. 36.

Weigel, D. and Nilsson, O. (1995). A developmental switch sufficient for flower initiation in diverse plants. *Nature* **377**: 495 – 500.