

Ecological Determinants of Life History Evolution of Two Indian Bamboo Species



Madhav Gadgil; S. Narendra Prasad

Biotropica, Vol. 16, No. 3. (Sep., 1984), pp. 161-172.

Stable URL:

<http://links.jstor.org/sici?sici=0006-3606%28198409%2916%3A3%3C161%3AEDOLHE%3E2.0.CO%3B2-H>

Biotropica is currently published by The Association for Tropical Biology and Conservation.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/tropbio.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Ecological Determinants of Life History Evolution of Two Indian Bamboo Species¹

Madhav Gadgil and S. Narendra Prasad

Center for Theoretical Studies, Indian Institute of Science, Bangalore 560 012, India

ABSTRACT

Almost all (70 out of 72) of the Indian bamboo species possess a long period of vegetative growth followed by a single suicidal bout of reproduction. Only about eight of these 70 monocarpic species exhibit synchronized seeding over an area of several hundred square kilometers. Of the two commonest species, *Bambusa arundinacea*, which forms dense stands along water courses in areas of less variable rainfall, belongs to this minority of synchronized seeders; *Dendrocalamus strictus*, which occurs in scattered numbers in areas of more variable rainfall, exhibits sporadic seeding behavior. Individuals of both species grow exponentially during the vegetative phase. Observations on the synchronized seeding of *B. arundinacea* show it to be spread over 5–6 years, with flower and seed production by any individual clump being completed over the dry season from December to April. An average clump produced 100 kg of seed, corresponding to 30 percent of its above-ground biomass. One major cohort of *B. arundinacea* widely distributed over peninsular India seeded in 1868–72, 1912–16, and 1958–62; while a number of minor cohorts have seeded at other times.

There is no defined direction over which seeding progresses in time. The bamboo seeds are subject to high levels of predation, and we propose that the exponential nature of clump growth in conjunction with predator swamping has led to the evolution of a long pre-reproductive period and monocarpy, which characterize most Indian bamboo species. Synchronized mast seeding is a further independent adaptation favored in a few species occurring in dense stands in more constant environments.

MOST BAMBOO SPECIES OF THE SEASONAL TROPICS and subtropics of the Indian-Asiatic region are notable for their long period of vegetative growth followed by a single suicidal bout of reproduction. Even more strikingly the populations of some of these species seed synchronously over large tracts. The majority of the species, however, do not seed in this synchronized fashion, but rather seed sporadically over their range (Brandis 1906, Troup 1921). Janzen (1976) first posed the question of the adaptive significance of this life cycle and concluded that the mast seeding serves the purpose of swamping predators (Lloyd and Dybas 1966). He postulated that the long pre-reproductive period, monocarpy, and synchrony all evolved together in response to predation and that asynchronous seeding in species like *Dendrocalamus strictus* is a secondarily derived condition resulting from human interference. Janzen also raised a number of intriguing questions about the seeding behavior of bamboos, for most of which he adduced few if any answers. In this paper, we present data that will answer some of these questions for two of the commonest monocarpic bamboo species of peninsular India, *Bambusa arundinacea* and *Dendrocalamus strictus*. We propose that Janzen's suggestion of the secondary nature of the sporadic seeding behavior of *D. strictus* is unlikely to be correct. Instead, we show that the long pre-reproductive phase and monocarpy must have evolved in response to predator swamping and the exponential

pattern of growth of bamboo clumps, and that synchrony is a further adaptation in species occurring in dense stands and in relatively constant environmental regimes.

MATERIALS AND METHODS

The results presented below are based on an ecological investigation of *B. arundinacea* and *D. strictus* over a five year period from April 1976 to February 1980 in the state of Karnataka in southern India (lat. 11°40'N to 18°22'N and long. 73°55'E to 78°40'E). Our investigations included estimations of population density, biomass, productivity as well as growth and mortality rates for both the species in 14 different localities in the state. We maintained notes on any sporadic seeding during the course of these investigations. Further observations were made on mast seeding by *B. arundinacea* of Sampaji forest range (lat. 12°30'N and long. 75°33'E) over the years 1976–80, including two periods of detailed observations in April 1979 and March 1980. We also examined all official documents of Karnataka Government, particularly the forest working plans for information on seeding of bamboo species in the state (Prasad and Gadgil 1981).

RESULTS AND DISCUSSION

DISTRIBUTION.—Under climax conditions, *B. arundinacea* is restricted to the formation of dense stands along water courses in localities with an annual rainfall of 1000–2000 mm, while *D. strictus* occurs in a wider variety of habitats

¹ Received 4 October 1982, Revised 28 September 1983, Accepted 3 November 1983.

in scattered populations in localities with an annual rainfall of 600–1500 mm. Rainfall, the major environmental parameter governing vegetation in seasonal tropics such as Karnataka, is much more variable in the drier habitats of *D. strictus*, with a coefficient of variation of around 0.4; this coefficient is uniformly around 0.2 in the higher rainfall tracts inhabited by *B. arundinacea* (Rao 1976). In keeping with its greater ecological amplitude in more variable habitats, *D. strictus* shows much greater morphological variation. Deogun (1937) recorded the existence of at least five varieties of this species in Karnataka differing in growth habit and thickness of culm wall.

Like all bamboos, *B. arundinacea* and *D. strictus* are shade intolerant and have profited from the opening of the forest canopy due to human interference. This has permitted *B. arundinacea* to colonize habitats away from water courses in localities with an annual rainfall of 1500–2000 mm, and *D. strictus* to form much denser stands than under climatic conditions in the drier habitats. When the British tremendously stepped up the pace of forest exploitation in India after the 1860's, they regarded bamboo as a weed, and forest working plans of the Karnataka state advocated its eradication from plantations as well as natural forest until the 1940's (Kadambi 1943). The villagers did, however, plant some bamboo on their farms and along irrigation channels, the preferred species being *B. arundinacea* in tracts of rainfall up to 1500 mm and *Oxytenanthera stocksii* in the wetter regions. Very limited forest plantations of bamboos—a few square kilometers in a few localities—were planted only after the 1930's. Contrary to the suggestion of Janzen (1976), there is absolutely no evidence of any significant change in the composition of forest populations of *D. strictus* or any other species by human agency in the state of Karnataka. Our reading of the literature for the rest of India, especially the forest working plans, indicates this to be true for the country as a whole.

LIFE CYCLE.—Both *B. arundinacea* and *D. strictus* are monocarpic, with a long period of vegetative growth followed by seeding and death of the clump. All species of bamboos are modular organisms. The term “clump” is customarily applied to a “genet” and “culm” to a “ramet” of bamboo species (McClure 1966). During our field work over the five years from 1976–80, we noticed many stray clumps of *D. strictus* in seed in many parts of the state; this, however, was not the case with *B. arundinacea*. Only one population of *B. arundinacea* in the Subramanya-Sulya-Sampaji tracts (lat. 12°30'N to 12°40'N, long. 75°22'E to 75°38'E) seeded synchronously as a whole over this period. We have no information on the genetic constitution of this population, which was dispersed over 4800 ha at an average population density of 100 clumps (genets) per hectare. All the

clumps observed died in the year following seeding. There was also a synchronous seeding of *D. strictus* populations near Katur (lat. 14°52'N, long. 75°02'E) beginning in 1981, after our systematic observations were concluded. These observations conform to the earlier records of consistently synchronous seeding in *B. arundinacea* and a combination of sporadic and synchronous seeding in *D. strictus* (Nicholson 1922, Deogun 1937, Gupta 1952, Mathauda 1952, Mathur 1964, Mohapatra 1969).

Figure 1 presents an analysis of the available records of two consecutive mast seedings by *B. arundinacea* and *D. strictus* (Prasad and Gadgil 1981). The range is from 26 to 64 years for *B. arundinacea* with over three-quarters of the records falling within the limit of 44 to 48 years. The lone record for 64 years from Walayar in Tamilnadu is suspect, because its second seeding of 1959–60 coincides with that of a widespread cohort which had seeded earlier, around 1912–16, and the record of an earlier seeding in 1896 may be in error. For *D. strictus* the range is wider, from 17 to 48 years, with a much less sharply defined mode around 36–40 years. This is in conformity with the more sporadic nature of seeding in *D. strictus*.

GROWTH.—Bamboos are grasses that have evolved into a tree form. The partitioning of biomass in a clump of *D. strictus*, namely leaves (8.8%), stem (69.9%), and rhizome and roots (22.3%), is very similar to the average partitioning of leaves (8%), stem (67%), and roots (25%) reported for a stand of trees in Thailand (Rodin and Bazilevich 1967, Patil 1979). In *B. arundinacea*, however, our observations show that about one-third of the biomass is underground. In bamboos the stems are green and participate in photosynthesis. Furthermore, the bamboos have a radically different pattern of growth compared to the other trees with which they compete. In a normal forest tree the growth is predominantly in height of the stem, so that the proportion of photosynthetic tissues to the structural tissues steadily declines with an increase in size, with a consequent decline in the relative growth rates of the tree (Prodan 1968, Evans 1972). The growth curve of a tree therefore conforms to the sigmoidal pattern.

Once a bamboo clump has passed through the seedling and bush stage, it begins to produce culms of the full adult height which reach the top of the canopy in a single, concentrated burst of growth lasting a few months. Beyond this stage, the growth of a bamboo plant is essentially by radial enlargement of the underground rhizome and addition of more and more culms, all of the same form. The proportion of photosynthetic tissue to the total biomass thus should change very little once a bamboo clump has been established. Consequently, the relative growth rate of an individual bamboo clump is ex-

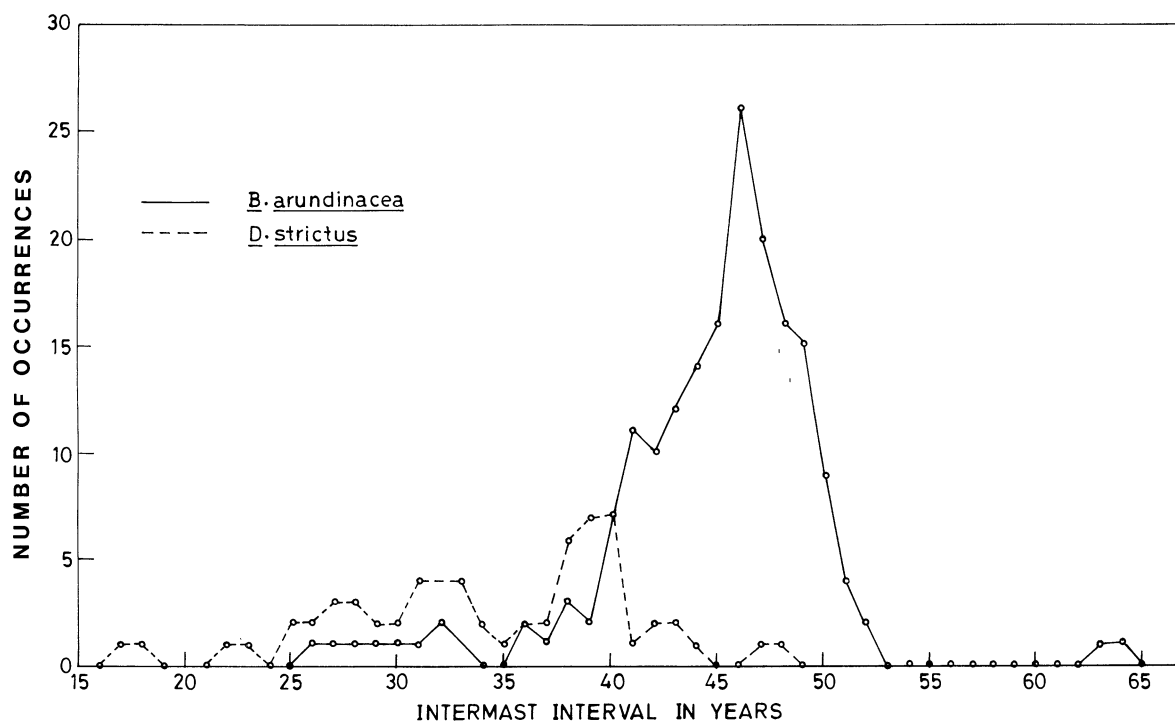


FIGURE 1. Frequency distribution of intermast intervals of *B. arundinacea* and *D. strictus*.

pected not to decline with size, but to remain constant. The bamboo clump as a whole should therefore exhibit an exponential pattern of growth.

The available data bear out this supposition. Kadambi (1949) monitored the total number of bamboo culms in three different plots over a period of 7 to 9 years beginning in 1935. A reanalysis of his data shows that the total number of culms in the population as a whole increased exponentially at the rate of about 4 percent per year over this entire period. Our own observations of individual *D. strictus* and *B. arundinacea* clumps over 3 years show that under protected conditions the number of culms per clump increases exponentially at the rate of 10 percent per year. The individual bamboo clump then exhibits exponential growth, presumably until the age of seeding, although the undisturbed populations accessible to us were 8–12 years old and therefore did not permit us to verify if the exponential growth slowed down with an increase in size. However, historical records exist of clumps with over 200 culms, suggesting that an exponential growth rate of up to 10 percent a year could very well have been maintained from the establishment of the clump at the age of 8–10 years until the age of seeding of 45–50 years (Rawlinson 1931).

PHENOLOGY.—The state of Karnataka receives most of its rainfall from the monsoons, with the rainy period varying from April–November in the southern part of the state to June–September in the northern part. The production of new culms begins about a month after the onset of the rains and continues until the end of the rainy period. The culms are produced year round in irrigated plantations. An individual culm completes its full growth in about 80 days.

We have detailed information on flower and seed production from the mast seeding of *B. arundinacea* in Sampaji range. Here, the rains last from May–October (Fig. 2). Flower production is initiated in the month of December, and the seeds ripen and fall in three waves over the dry season. The first wave of seed fall lasts for 3 weeks in February, accounting for 20 percent of the total seed collected by the local villagers; the second wave, for 2 weeks in the month of March, accounting for 30 percent of the total seed collected by villagers; and the last wave, for 2–3 weeks in April, accounting for the remaining 50 percent of seed production. These observations agree with those of Nicholson (1945), who studied *B. arundinacea* populations in the state of Orissa in eastern India. The bamboo clump dries completely within

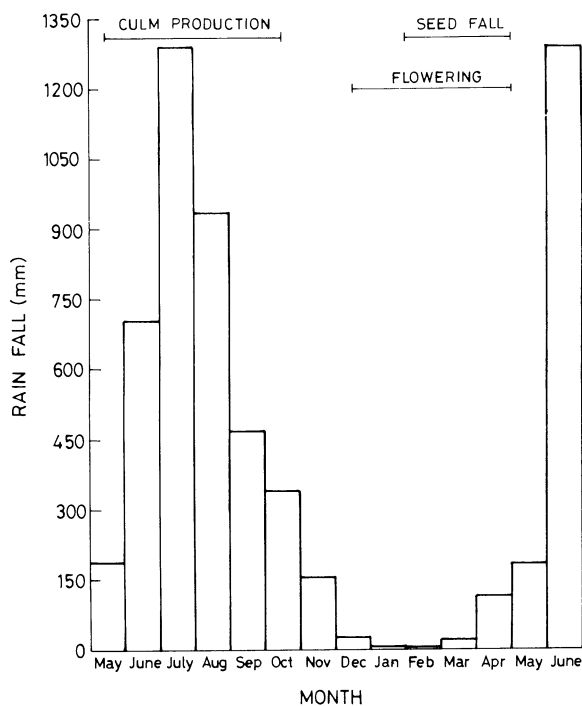


FIGURE 2. Mean monthly rainfall and phenology of *B. arundinacea* at Sampaji.

a couple of months after cessation of seed production. The seeds germinate at the onset of the rains in May and June, forming an incredibly thick carpet of seedlings on the ground, particularly by the side of the water courses. There is no dormancy and the viability of seeds is down to 5 percent within 6 months.

The phenology of *D. strictus* follows the same pattern of new culm production over the monsoon, flower and seed production over the dry season, and death of the parent clump by the next monsoon.

SEED PRODUCTION AND REPRODUCTIVE EFFORT.—Our observations at Sampaji revealed that a *B. arundinacea* clump produces an astronomical number of flowers. At each node of a culm there was an average of 133 spikes, and each spike had an average of 156 flowers. Since a single culm had an average 65 flower-bearing nodes, each culm bore some 1.3 million flowers. Some of the bigger clumps had as many as 52 culms in this population; *B. arundinacea* clumps with as many as 200 culms have been recorded. Thus, even in this population, a single individual produced as many as 68 million flowers. Of the seeds fallen on the ground, about 24 percent had a developed endosperm. Each bamboo culm thus may be estimated to produce 312 000 fully developed seeds; since each seed

TABLE 1. Yearly distribution of spatial extent of mast seeding of *Bambusa arundinacea* populations in North Karnataka.

Year	Extent of mast seeding (km ²)
1863-64	743.4
1864-65	—
1865-66	289.7
1866-67	1405.4
1867-68	—
1868	877.2
1868-69	813.1
1869-70	—
1870-71	—
1871-72	—
1872-73	1110.8
1868-75	723.3
Total	5962.9

weighed 0.012 g, this comes to a seed production of 3.744 kg per culm.

In the mast seeding population we observed, an average bamboo clump had 23 culms, so that an average bamboo plant could be estimated to have produced 86 kg of seeds. This agreed very well with the estimate of the local villagers, who had carefully collected seed under selected clumps throughout the season. Their estimate came to 4 to 4.5 kg of seeds per culm, or a total of 92 to 103.5 kg for an average clump with 23 culms. We also estimated the amount of bamboo seeds accumulated under two clumps by 5 April 1979, when three-quarters of the total production was reported to have been completed by the villagers engaged in bamboo seed collection. Our estimate came to 1.2 kg per culm. Since a significant fraction of the seeds accumulating since February is expected to have been destroyed by seed predators, this estimate agrees well with the expectations.

Using the regressions of culm diameter and number of internodes on culm dry weight, we can estimate the average weight of a culm in this Sampaji population as 13 kg. Further, the ratio of underground to above-ground biomass for *B. arundinacea* is 1:2 (Prasad and Gadgil 1981). The ratio of seed weight to dry weight of aerial biomass is about 0.3 and to total biomass about 0.2. This ratio falls in the range for *r*-selected herbaceous plants or most grain crops and is well above the upper limit of the range for trees (Harper, Lovell, and Moore 1971, Abrahamson and Gadgil 1973).

SEED PREDATION.—Like most other grasses, bamboos produce seeds that are highly palatable to a number of animals, including pheasants, rodents, deer, wild pigs and possibly the Indian elephant (Troup 1921, Soderstrom and Calderon 1974, Janzen 1976). Since a single clump

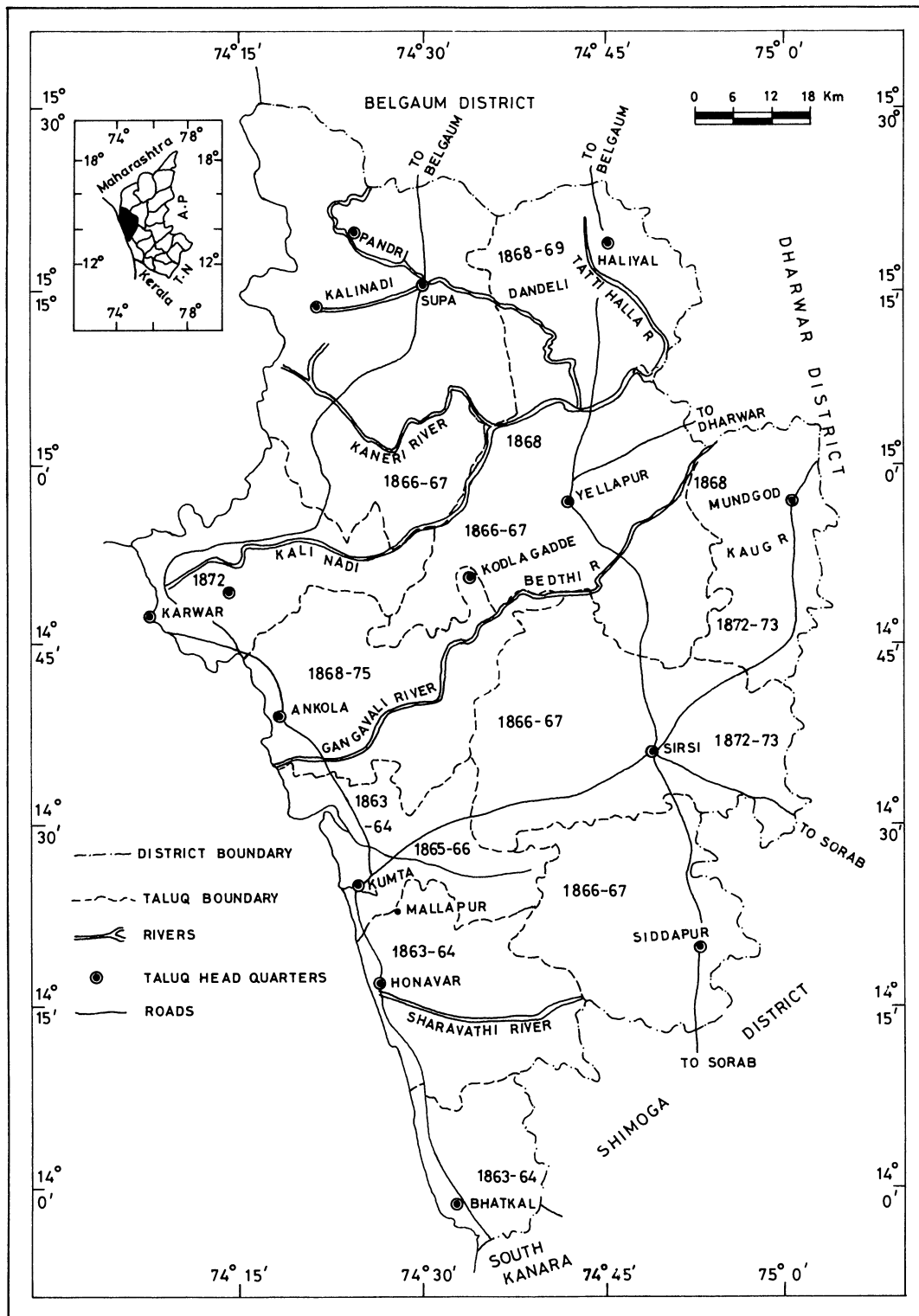


FIGURE 3. Mast seeding of *B. arundinacea* populations during 1863-75 in North Kanara.

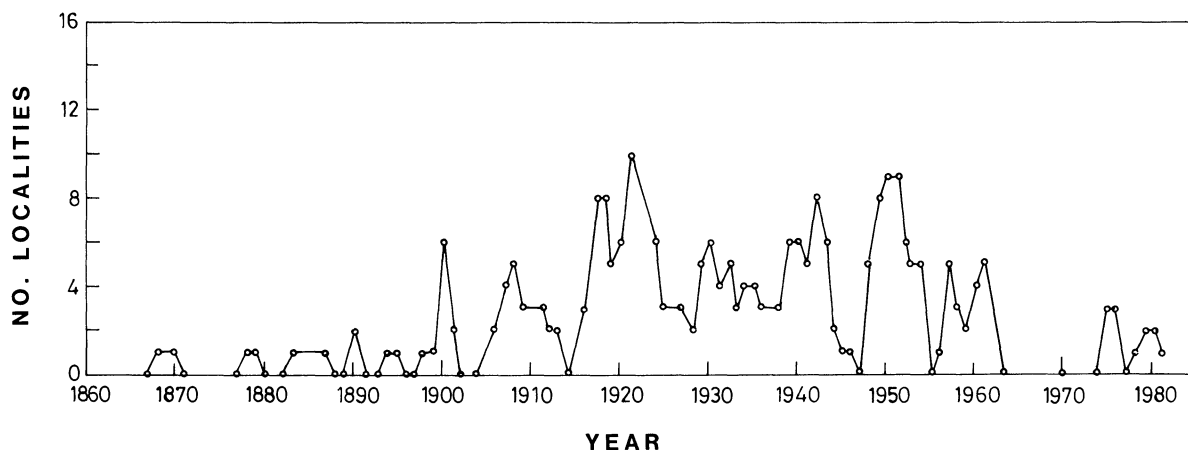


FIGURE 4. Yearly mast seeding of *D. strictus*.

may produce as many as 100 kg over a few months, and there may easily be as many as 100 clumps per hectare, the seed production may amount to 1 kg per every square meter—a veritable bonanza. Moreover, this seed production takes place in a deciduous forest, where under climax conditions relatively few fleshy fruits or palatable seeds are produced. As Janzen (1976) points out, predation on these seeds must have been an important evolutionary force, and it is therefore of much interest to estimate the magnitude and time course of this predation.

We have only a limited amount of data on the predation of *B. arundinacea* seeds near the peak of seeding in 1979, thus leaving unanswered the significant question of the relative magnitude of predation on the peak versus the tails of seed production curves. As noted above, we estimated the seed accumulation under the clumps by 5 April 1979, when about 75 percent of the total seed production was over, by the estimates of the local villagers. The amount of seed still present under the clumps that the villagers had left undisturbed was about 40 percent of the quantity they had obtained through regular daily collections. This suggests that about 60 percent of the fallen seed had been destroyed over the 2-month period from mid-February to mid-April. As larger herbivores were eliminated from this forest tract, the main agents of this predation are likely to have been rodents and gallinaceous birds (*e.g.*, partridges, jungle fowl, quails).

We also collected newly fallen seeds over a period of 10 days in April 1978. Of these, 63 to 69 percent had no endosperm, 6 to 7 percent were damaged by birds, and 3 to 5 percent had insect emergence holes. We actually observed several species of fringillid birds feeding on bamboo seeds in large flocks. These birds may ingest the majority of seeds in their entirety, leaving a small number of them in a damaged condition. A number of

insects also emerged later from seeds stored from this collection, so that the eventual insect damage must be much more than 3 to 5 percent.

The villagers of the Sampaji range collected a certain amount of bamboo seeds for sale to the forest department, as well as for domestic consumption. The amounts of seed collected annually by one villager from 1977 through 1981 were: 200 kg, 400 kg, 400 kg, 600 kg, and 100 kg. These were collected from just a few clumps by clearing the ground under them. The total amount collected from the whole locality was less than 1 percent of the total seeds being produced. Man was therefore not a very significant predator on bamboo seeds in this locality, and this is likely to have been so throughout the historical period.

There are, however, accounts of enormous amounts of seeds being collected when a famine coincided with mast seeding of bamboo. Two earlier records of such an occurrence exist for the state of Karnataka, involving large-scale migrations of people from famine-stricken areas to collect seeds of *B. arundinacea* in Supa in 1865 (Campbell 1883) and Sagar in 1966–1967 (H. R. Bhat, pers. comm.). Janzen (1976) quotes other records of such human collection of bamboo seeds in India, including that of *D. strictus*. These must have been sporadic occurrences, however; there is no evidence that bamboo mast seeding always accompanies drought years, as has been suggested. There was no famine at the time of the very widespread mast seedings of *B. arundinacea* in peninsular India over 1912 to 1916 and 1958 to 1962, and no records of any extensive collection of seeds during this period. Since such collection on a massive scale is apparently related to the occurrence of famine elsewhere, it may not necessarily have fallen on the peak years of seeding rather than the tails of seeding distribution.

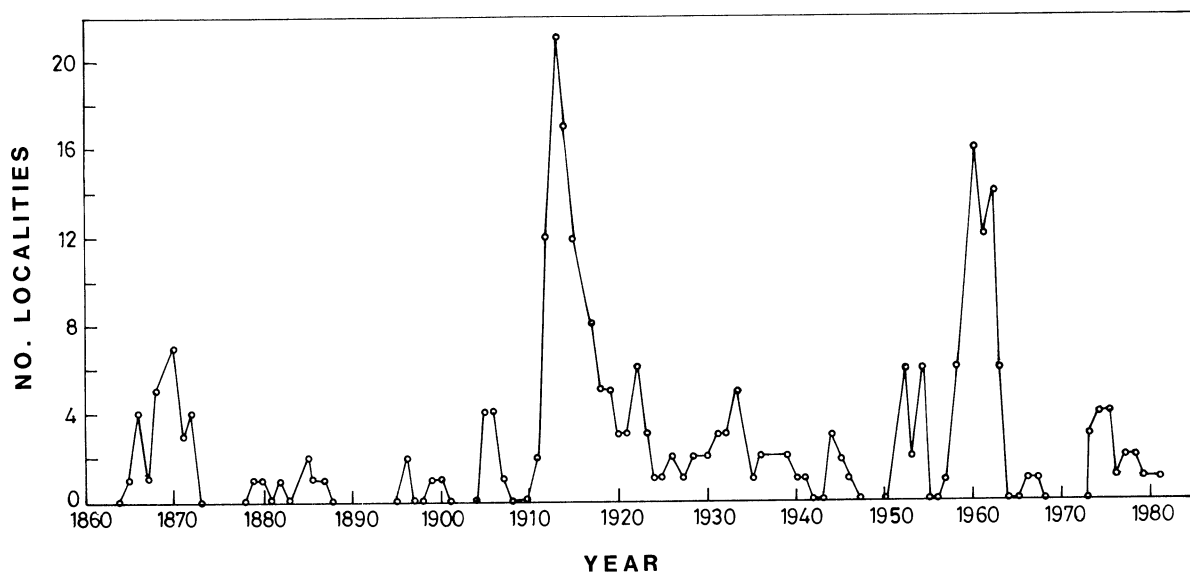


FIGURE 5. Yearly mast seeding of *B. arundinacea*.

One may speculate here on the very large fraction—about 65 percent—of seeds without a developed endosperm. Such seeds may simply relate to the impossibility of securing any higher levels of pollination. Alternatively, they may help reduce the predation on fertile seeds by forcing seed predators to waste part of their energy on sifting through a lot of chaff.

COURSE OF A MAST SEEDING.—We have 124 records of mast seeding in *B. arundinacea* and 122 in *D. strictus* (Prasad and Gadgil 1981). Nearly 70 percent of these record the seeding for one or two years, while only about 8 percent record it as being spread over more than five years. The mast seeding of *B. arundinacea* we observed at Sampaji began with a few clumps coming into seed in 1976, with the vast majority seeding in 1978, 1979, and 1980 and the last few stragglers seeding in 1981. Reliable observers who have witnessed other mast seedings also report it as lasting over 4–5 years. It has been suggested that the mast seeding of *B. arundinacea* spreads like a wave in a definite direction, taking a few years to extend over the whole flowering area (Troup 1921). The best information pertaining to this point is available from the Uttar Kannada (earlier known as North Kanara) district of Karnataka from the records of the District Gazetteer compiled soon after the mast seeding of 1863–1875 (Campbell 1883). While there likely is some inconsistency in how the dates of seeding are recorded with the spread, such as 1868–75 for Ankola (including all the tail years) and 1872 for Karwar (only the peak year), the information appears on the whole to be very carefully

compiled. It is all the more valuable because this was and continues to be one of the most thickly forested districts of peninsular India.

Table 1 gives the yearly distribution of the spatial extent of mast seeding, which varies from 290 to 1110 km². This may be compared to the extent of 565 km² over Bhagamandala-Sampaji-Sulya-Subramanya ranges for the mast seeding of 1976–81 that we observed. Figure 3 shows conclusively that there was no particular direction in which the wave of mast seeding spread from year to year.

MAST SEEDING COHORTS.—Finally, we may consider the evidence for synchrony in mast seeding on spatial scales greater than those of a few hundred square kilometers mentioned above. For this purpose, we consider the number of localities reporting mast seeding of *D. strictus* or *B. arundinacea* over peninsular India in any given year. Since records for the 19th century are somewhat incomplete, the three oldest records of mast seeding of *B. arundinacea* in 1804, 1812, and 1818 have been left out of Figures 4 and 5, which present the rest of the available information.

If mast seeding in one locality is independent of what happens in other localities, the number of localities reporting seeding in any given year is expected to follow a Poisson distribution with variance equalling the mean. This is not the case for either of the species. The mean number of localities reporting seeding in a year is very similar: 3.185 for *D. strictus* and 3.222 for *B. arundinacea*. The variance is 7.064 for the former and 18.716

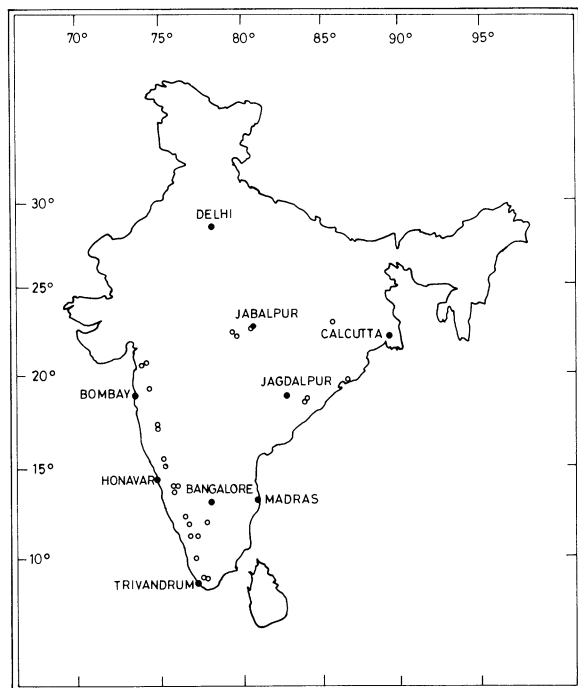


FIGURE 6. Geographical distribution of dominant mast seeding cohort of *B. arundinacea* in peninsular India.

for the latter. Thus, while both species show a greater incidence of mast seeding in certain years than is expected by chance alone, such concentration of seeding is much more pronounced in the case of *B. arundinacea*. Considering four consecutive years in periods of concentrated seeding, as many as 60 and 53 localities report seeding in the case of *B. arundinacea*, while only 32 do so in the case of *D. strictus*. The former deviates markedly from what is possible randomly and suggests that there is a strong correlation in the incidence of seeding for a number of different localities in *B. arundinacea*. In fact, there appears to be one dominant cycle of mast seeding of *B. arundinacea* with peaks in 1868–72, 1912–16, and 1958–62 over much of peninsular India. The intermast intervals of 44 and 46 years between these peaks correspond to the well-defined mode depicted in Figure 1. Figure 6 shows geographical distribution of the localities, most of which are in common for these mast seedings of 1868–72, 1912–16, and 1958–62.

There are no such well-marked peaks of seeding for *D. strictus*. One possibility is that a widespread cohort seeded in 1920–23 and again in 1947–51. However, an examination of the actual localities involved shows that very few seeded at both times; for *B. arundinacea*, in contrast, many localities were in common for the three consecutive large-scale seedings.

One is then tempted to speculate that the entire pen-

insular Indian population of *B. arundinacea* may have originated from a single mast seeding cohort. As the cohort spread over India, some populations inhabiting isolated pockets may have assumed seeding at other times, perhaps due to mutants among the founders. Figure 7 shows the extent and dispersion of four such known cohorts co-occurring with the dominant cohort in the state of Karnataka. There is no evidence of any systematic spatio-temporal progression of mast seeding on this scale, either.

ENVIRONMENTAL CLUES.—The occasional but striking coincidence of mast seeding with conditions of drought in certain areas has given rise to the notion that such seeding is prompted by low rainfall. There is, however, no real evidence for this. An examination of the rainfall records for Karnataka in fact indicates a slight excess of good rainfall years both preceding and coinciding with seeding of either bamboo species in a given locality, although this is not significant statistically (Parthasarathy and Mooley 1981).

LIFE HISTORY EVOLUTION.—Three intriguing questions arise in connection with the life histories of the Indian bamboo species: (1) Why do almost all species, some 70 out of 72, seed just once and die? (2) Why do most species wait so long, from 12 to 60 years or more, before they seed? (3) Why do some, about 7 or 8 of these 70 monocarpic species, seed synchronously over large areas? Janzen (1976) attempts to answer all these questions in terms of predator swamping. He adduces considerable evidence of extensive predation, by both sedentary and nomadic predators, on bamboo seeds. He suggests that a bamboo plant will minimize the risk of mortality suffered by each of its seeds by producing these seeds in enormous quantities and in synchrony with other members of the population, so that many seeds will escape after fully satiating the predator population. Since large seed crops may be produced by vegetatively growing for a long time and then throwing all the reserves into one ultimate effort of breeding, this would simultaneously favor monocarpy as well as a long pre-reproductive period, along with the synchrony of seeding by a whole population. As a corollary he regards the sporadic seeding by species like *D. strictus* as a secondarily derived condition due to human predation concentrating on peaks of seeding and humans mixing up different mast seeding cohorts.

While Janzen's central hypothesis of the role of predator swamping is attractive, there are difficulties in accepting his entire argument. First, the vast majority of the species are sporadic rather than synchronous seeders, indicating that monocarpy with a long pre-reproductive period need not always go together with mast seeding. Second, there is simply no evidence for the kind of human interference Janzen postulates. In Karnataka at least, contrary to expectations on this hypothesis, it is the synchro-

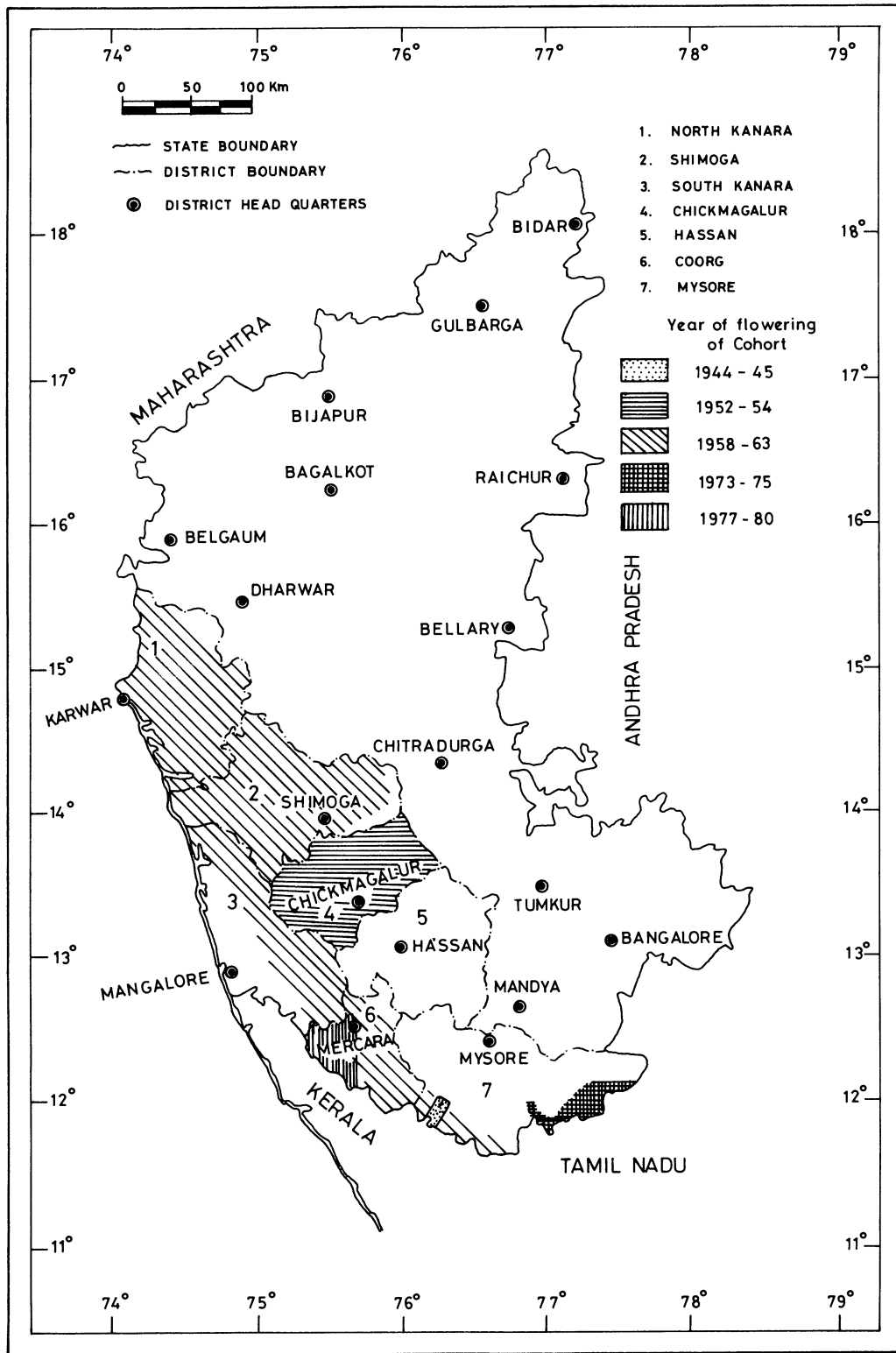


FIGURE 7. Geographical distribution of known mast seeding cohorts of *B. arundinacea* in Karnataka.

nous-seeding *B. arundinacea* rather than the sporadic-seeding *D. strictus* that is somewhat susceptible, though to a minor degree, to the kind of interference invoked by Janzen in explaining the secondary evolution of sporadic seeding. We therefore postulate that a long pre-reproductive life and monocarpy are common adaptations evolved by most bamboo species in seasonal tropics, while synchrony of seeding by an entire population is a further independent adaptation evolved by a few of these species because of some special features of their ecological setting.

The forces molding these parameters are best elucidated in terms of the so-called reproductive effort model of the evolution of life histories (Gadgil and Bossert 1970, Schaffer and Gadgil 1975, Schaffer and Rosenzweig 1977, Charlesworth 1980). This model considers a plant as possessing a limited amount of resources, such that any allocation of resources leading to higher seed output at a given age incurs costs in lower survivorship and vegetative growth (for reproduction at future ages). In other words, b_i is a monotonically increasing function of E_i , while p_i and V_{i+1}/V_0 are monotonically decreasing functions of E_i . Here:

- E_i —reproductive effort at age i is the fraction of available resources allocated to reproduction
- b_i —fertility at age i
- p_i —probability of survival from age i to $i + 1$
- $\frac{V_{i+1}}{V_0}$ —reproductive value as defined by Fisher at age $i + 1$.

The reproductive value, which for simplicity will be referred to as V_{i+1} from now on, is a measure of the contribution to population growth by all individuals of age $i + 1$. This will be lowered if growth and, therefore, ability to reproduce or survive beyond age i is reduced. The product $p_i V_{i+1}$ has been termed residual reproductive value.

Natural selection is then expected to maximize the sum:

$$b_i + p_i V_{i+1}$$

and the reproductive effort E_i favored at any age will be that which achieves this (Fig. 8). In terms of this model, a monocarpic life cycle with a long pre-reproductive period will be that in which optimal E_i is zero for many initial ages, and one for some advanced age.

The significance of the exponential growth pattern of bamboo clumps becomes clear in the context of this model. This growth pattern implies a substantial cost in terms of future reproduction, if reproduction at an early age cuts into growth. In terms of the model, b_i , the current fecundity, will be rather low compared to $p_i V_{i+1}$, the residual reproductive value, so that a zero reproductive effort will be optimal (Fig. 8a). As Hamilton (1966) has

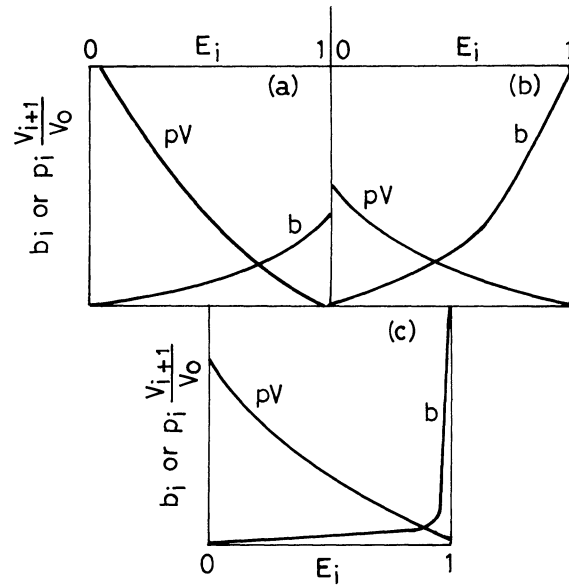


FIGURE 8. Possible configurations of current fecundity (b_i) and residual reproductive value ($p_i[V_{i+1}/V_0$]) as functions of reproductive effort (E_i). The optimal reproductive effort will be zero for (a) and one for (b) and (c).

shown, this balance gradually will shift in favor of higher reproductive effort as the organism ages even if the growth were to continue exponentially (Fig. 8b). In addition, as the bamboo clump grows, a larger proportion of the culms will be crowded in the center and will be unable to photosynthesize properly, thereby further reducing the cost incurred by cutting into growth.

Thus, while the exponential growth patterns will favor a long pre-reproductive period, the reproduction once commenced need not be total, leading to monocarpy. Monocarpy will be favored when the b_i and $p_i V_{i+1}$ are convex functions of E_i . In other words, monocarpy is favored when every additional reproductive effort brings greater returns in terms of effective reproduction, and every additional reproductive effort is attended upon by lower cost in terms of future survival and reproduction. As Schaffer and Rosenzweig (1977) point out, predator swamping implies the first of these conditions, since every additional seed produced stands a better chance of escaping predation. Predator swamping thus favors monocarpy, but will not guarantee it unless the second condition also is fulfilled. We suggest another mechanism which will generate a form of $b_i(E_i)$ curve which will guarantee monocarpy: the role of death of parent in affecting the survival of seedlings. Bamboos are light-demanding plants that grow in a forest with a closed canopy under climax conditions. The opening of the canopy therefore would make

a tremendous difference to the chance of survival of the seedling. A suicidal bout of breeding followed by the death of the parent creates such a gap in the canopy and therefore may generate b , as an extremely convex function of E , favoring monocarpy regardless of the form of $p_i V_{i+1}(E_i)$ curve (Fig. 8c).

Our suggestion is that (a) the exponential form of growth of a bamboo plant, (b) the critical role of death of the parent in ensuring the survival of seedlings, and (c) progressive reduction in risk of seed predation with increasing seed output all would favor the evolution of a monocarpic life cycle with a long pre-reproductive period, a common feature of almost all bamboo species in seasonal tropics and subtropics. Given this, the evolution of synchronous mast seeding will depend on two other factors: the extent to which predators on seeds of one individual will prey on seeds of another individual, and year-to-year variation in the probability of success of seeds and seedlings due to fluctuations in parameters such as rainfall. If individuals of a species are so scattered that predators on seeds of one individual or its progeny are unlikely to prey on the seeds of another individual, there will be no special advantage for members of a population to seed in synchrony. In fact, it may be advantageous for a plant to program its offspring to reproduce in different years if there is wide year-to-year fluctuation in germination or seedling survival success, so that at least some of its grand-offspring are born in a favorable year (cf. Murphy 1968). *D. strictus*, known for its often sporadic seeding, occurs at low densities under climax conditions and is character-

istic of regions of more fluctuating rainfall regimes. Furthermore, *D. strictus* appears to occur in several different ecotypes, each of which may have a different length of life cycle. The asynchronous seeding of *D. strictus* therefore is much more plausibly explained as fitted to its particular ecological niche, rather than as a recent, secondarily derived condition.

Bambusa arundinacea, on the contrary, occurs in dense stands lining the water courses under climax conditions and inhabits more constant environmental regimes. In such a dense stand, there would be definite advantage to the whole population seeding in synchrony in swamping predators. Furthermore, the death of the whole population and the great forest fires that follow enhance the chances of survival of the seedlings. The last proposition need not invoke group but only kin selection if the individuals in a stand are closely related, as appears possible. The mast seeding of *B. arundinacea* may then be a further adaptation over and above monocarpy following a long pre-reproductive period.

We have tried to set down in this paper some of our observations on this fascinating biological phenomenon. Unfortunately these observations have been limited, and carried out in habitats which are now very different from those in which bamboos must have originally evolved. Nevertheless, the recording that is possible is a matter of "urgent ecology," for even these last populations in changed habitats are fast approaching decimation, and there may be no bamboos left for the next grand flowering slated for A.D. 2005! (Gadgil and Prasad 1978).

LITERATURE CITED

- ABRAHAMSON, S. G., AND M. GADGIL. 1973. Growth form and reproductive effort in Goldenrods (*Solidago*, compositae). Amer. Nat. 107: 651-661.
- BRANDIS, D. 1906. Indian trees. Bishen Singh, Mahendra Pal Singh, Dehra Dun.
- CAMPBELL, J. M. 1883. Bombay gazeteer: Kanara 25(1), Government Central Press, Bombay.
- CHARLESWORTH, B. 1980. Evolution in age structured populations. Cambridge University Press, London.
- DEOGUN, P. N. 1937. The silviculture and management of the bamboo, *Dendrocalamus strictus*. Indian Forest Records (New Series) 2(4): 75-173.
- EVANS, G. C. 1972. The quantitative analysis of plant growth. Blackwell, London.
- GADGIL, M. D., AND W. H. BOSSERT. 1970. Life historical consequences of natural selection. Amer. Nat. 104: 1-24.
- , AND S. N. PRASAD. 1978. Vanishing bamboo stocks. Commerce 136 (3497): 1000-1004.
- GUPTA, M. 1952. Gregarious flowering of *Dendrocalamus strictus*. Indian Forester 78: 547-550.
- HAMILTON, W. D. 1966. The moulding of senescence by natural selection. J. Theor. Biol. 12: 12-45.
- HARPER, J. L., P. H. LOVELL, AND K. G. MOORE. 1970. The shapes and sizes of seeds. Ann. Rev. Ecol. and Syst. 7: 327-356.
- JANZEN, D. H. 1976. Why do bamboos wait so long to flower? Ann. Rev. Ecol. and Syst. 7: 347-91.
- KADAMBI, K. 1943. A revised working plan for the forests of Bhadravati division. Working plans, Forest Department, Government of Karnataka, Bangalore.
- . 1949. On the ecology and silviculture of *Dendrocalamus strictus* in the bamboo forests of Bhadravathi division, Mysore State and comparative notes on the species of *Bambusa arundinacea*, *Ochlandra travancorica*, *Oxytenanthera monostigma* and *O. stocksii*. Indian Forester 75: 289-299.
- LLOYD, D. M., AND H. S. DYBAS. 1966. The periodical cicada problem. II. Evolution. Evolution 20: 466-505.
- MATHAUDA, G.S. 1952. Flowering habits of the bamboo, *Dendrocalamus strictus*. Indian Forester 78: 86-88.
- MATHUR, R. S. 1964. Bamboo potential and productivity with particular reference to Raigarh forests. Proc. All Indian bamboo study tour and symposium, Forest Research Institute, Dehra Dun.
- MCCLURE, F. A. 1966. Bamboos: a fresh perspective. Harvard University Press, Cambridge, Mass.

- MOHAPATRA, S. 1969. Observations on bamboo flowering. *Indian Forester* 95: 213.
- MURPHY, G. I. 1968. Pattern in life history phenomena and the environment. *Amer. Nat.* 102: 52-64.
- NICHOLSON, J. W. 1922. Note on the distribution and habit of *D. strictus* and *B. arundinacea* in Orissa. *Indian Forester* 48: 425-428.
- . 1945. Flowering of *Bambusa arundinacea* in Orissa. *Indian Forester* 71: 435-436.
- PARTHASARATHY, B., AND D. A. MOOLEY. 1981. Hundred years of Karnataka rainfall. Indian Institute of Tropical Meteorology, Poona.
- PATIL, V. C. 1979. Unpublished Ph.D. Thesis, Agricultural College, Dharwar, Karnataka.
- PRASAD, S. N., AND M. GADGIL. 1981. Conservation of bamboo resources of Karnataka. Karnataka State Council for Science and Technology, Bangalore.
- PRODAN, M. 1968. Forest biometrics. Pergamon Press, Oxford.
- RAO, Y. P. 1976. Southwest monsoon. Meteorological monograph synoptic meteorology No. 1/1976. India Meteorological Department, New Delhi.
- RAWLINSON, H. G. (ED.). 1931. Captain Basin Hall's travels in India, Ceylon and Borneo. George Routledge, London.
- RODIN, L. E., AND N. I. BAZILEVICH. 1967. Production and mineral cycling in terrestrial vegetation. Oliver and Boyd, Edinburgh.
- SCHAFFER, W. M., AND M. GADGIL. 1975. Selection for optimal life histories in plants. In M. Cody and J. M. Diamond (Eds.). Ecology and evolution of communities, pp. 142-157. Harvard University Press, Cambridge, Massachusetts.
- , AND M. L. ROSENZWEIG. 1977. Selection for optimal life histories II. Multiple equilibria and the evolution of alternative reproductive strategies. *Ecology* 58: 60-72.
- SODERSTROM, T. R., AND C. E. CALDERON. 1974. Primitive forest grasses and the evolution of the bambusoideae. *Biotropica* 6: 141-153.
- TROUP, R. S. 1921. Silviculture of Indian trees. Clarendon, Oxford.
-

Plan for the ATB Meeting, 1985

The Association for Tropical Biology will hold its annual meeting for 1985 with The American Institute of Biological Sciences (AIBS), at the University of Florida, Gainesville, August 11-15. This should be one of ATB's most exciting meetings, attracting many tropical biologists. People with ideas for symposia should contact Dr. Terry Erwin, Dept. of Entomology—MNH, Smithsonian Institution, Washington, D.C. 20560, as soon as possible. Those interested in presenting a contributed paper should obtain forms for abstracts from Dr. Laurence Skog, Department of Botany, NHB 166, Smithsonian Institution, Washington, D.C. 20560 U.S.A.