Y. Widmer*: **Flowering Phenology of *Chusquea* Bamboos with Special Reference to *Chusquea talamancensis* in Costa Rica**

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Abstract

Mass flowering of *Chusquea talamancensis* Widmer & L.G. Clark, *C. tomentosa* Widmer & L.G. Clark, and *C. subtilis* Widmer & L.G. Clark was observed in the Cordillera de Talamanca, Costa Rica from 1987 to 1990. These wind-pollinated bamboos are semelparous after growing vegetatively for at least three decades. There is no seed production when isolated plants flower; seedlings appear only after mass flowering, indicating that reproductive success depends on cross-pollination. The different phenological states are coupled with the seasonal rainfall pattern. Flower formation, fruit formation and germination of seeds occur in the rainy season, whereas pollination, fruit maturation and abscission occur in the dry season. In the montane forests *Chusquea talamancensis* seeds germinate two years after flowering and then the forest floor is covered with seedlings. In the large population of *Chusquea talamancensis*, different flowering phases were recognized. Preliminary sporadic flowering was followed by mass flowering in two cohorts on successive years, though some isolated plants remain in the vegetative condition and may flower out of phase.

Introduction

Most woody bambusoid grasses are semelparous; i.e. the life cycle of the plant ends with flowering, and interfloral periods may extend over 15 - 60 years. Temperate bamboos flower even at intervals of 100 years (Numata, 1974). There are several different evolutionary hypotheses to explain bamboo life cycles, semelparity, and synchronism within the flowering population (Kawamura, 1927; Uchimura, 1980; Campbell, 1985). To date, the most generally accepted hypothesis is the consumer satiation or predator-escape hypothesis where the long interfloral period is interpreted as a response to predation by animals, as a "mechanism for escape from seed predators through satiation" by means of a high seed production (Janzen 1976, 1985). Campbell (1985) summarizes the life-cycles of bamboos as follows: (a) continual or seasonal yearly flowering, without mortality; (b) sporadic flowering at irregular intervals, generally with some recovery of the clone or in other cases with complete mortality; (c) periodic mass flowering at approximately regular intervals, generally with mortality, in some cases with partial survival of the weakened rhizomes. Still, the understanding of the life-cycles of bamboos is not conclusive, not only because of the time factor, but because the records for one species are mostly fragmentary and geographically dispersed, and herbarium specimens often lack information about the extent and the phenological stage of the flowering process. When records of bamboo flowering are compiled, there is rarely any distinction made between bamboo growing in its natural environment and bamboo growing in areas with significant human impact or in cultivation. Data on bamboos at anthropogenically disturbed sites, following logging, burning, and grazing, as well as cultivated bamboos (usually obtained from vegetative propagation) provide only a partial understanding of the flowering process because of their uncertain history and often unknown provenance. Management practices can change the intrinsic characteristics of bamboos (e.g. the periodicity of flowering). For example, Liao (1990) found that *Phyllostachys pubescens* which has been intensively propagated vegetatively rarely flowers because the long-term vegetative growth is continued, and further, that a flowered stand often recovers vegetatively if it is artificially watered and fertilized. Observations on a native bamboo species that is established in a natural community may facilitate the interpretation of the flowering and seeding process. McClure (1966) refers to this point indirectly: "abundant yields occur only in a few species out of hundreds observed

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in flower; and these are principally bamboos not under cultivation."

The aim of this study is to offer information on the flowering and seeding process of some *Chusquea* species which grow naturally as understory in the oak forests of the Cordillera de Talamanca. The research on *Chusquea* bamboos in Costa Rica was initiated in 1985 by the CATIE (Centro Agronómico Tropical de Investigación y Enseñanza) project "Silviculture of Natural Forests." This project is working on a sustainable management plan of the montane forests and was therefore interested in the study of the ecology of the *Chusquea* bamboos. Unexpectedly, during the investigation between 1987 and 1990, flowering of several *Chusquea* species was spreading gradually across the study area. In total, six *Chusquea* species showed mass flowering in the Cordillera de Talamanca (Widmer 1994). The present paper deals with three species described by Widmer and Clark (1991): *Chusquea talamancensis, C. tomentosa* and *C. subtilis.* It was a rare and unexpected opportunity to observe bamboo mass-flowering over an area of almost 30 km² of largely undisturbed forest.

Study Site

The observations on flowering phenology of the three *Chusquea* species were carried out on the Atlantic side of the Cordillera de Talamanca in the area of Cerro Asunción, La Georgina, Cerro Abarca, Villa Mills, and Cerros Cuericí, Province of Cartago (Figure 1). The area is part of the Costa Rican System of National Parks and Forest Reserves and is predominantly covered by old-growth forest with *Quercus* species dominating. The understory *Chusquea* species in this mountainous region are woody, clump-forming bamboos with pachymorph (sympodial) rhizomes. *Chusquea talamancensis* and *C. tomentosa* are the most widely distributed species at altitudes from 2600 to 3100 m. *Chusquea subtilis* is more patchily distributed and confined to more humid sites near streams at altitudes from 2500 to 2800 m (Widmer, 1994). Mean annual rainfall at Villa Mills weather station is 2610 mm (Figure 2). The dry months are January to March when mean monthly rainfall ranges from 20 - 35 mm. Most rain falls between May and November, mean monthly rainfall between 250 - 470 mm. From 1987 to 1989 the mean annual air temperature was 8.2°C, with mean daily temperature variation of 9.4 - 10.3°C in the dry season and 7.5 - 8.5°C in the rainy season. Mean maximum temperatures reached up to 14.4°C in April and minimum temperatures down to 3.1°C in January (data from the Instituto Costaricense de Electricidad).

Materials and Methods

The inflorescences of randomly selected plants were monitored to observe the phenological sequence. The spikelets (Figure 3) were collected and opened to determine the phenological state. Voucher specimens (Table 1) were made and classified as incipient flower, immature flower, mature flower, incipient fruit, immature fruit, mature fruit, and empty (vain) flowers. Quantitative data on the flowering of *Chusquea talamancensis, C. tomentosa,* and *C. subtilis* were gained from a survey made from CATIE plots between October - November, 1989. The plots were situated between Cerro Abarca and Cerro Cuericí at altitudes from 2650 to 2830 m. They included 21 randomly-placed plots and, in addition, a grid of nine 1-ha plots (Figure 1, dots and squares, respectively). Bamboo clumps were counted along a 4 x 100 m band on the center line of the plot. The phenological state of each clump was determined on the basis of the spikelet (Table 2) and voucher specimens were collected. In March 1990, an extensive survey was carried out in the fifty-three 100 m² plots of the author's ecological study using the same methods described above. To estimate seed production, 100 panicles were collected in March 1990 from two clumps of *Chusquea talamancensis* in La Georgina and in Cerros Cuericí, respectively. The panicles were dried for 3 days, then shaken and scrubbed.

Seeds were separated through water immersion for 24 hours; the viable seeds sank (while the non-viable seeds floated), and their wet and dry weight were determined. Viability of the seeds of *Chusquea talamancensis* was further tested *in vivo* and *in vitro* at the CATIE facilities. Seeds collected in January 1990 were kept in a cool chamber intended for seed collections. Some seeds were sown in February 1990 on a germination bed with sand under warm (22°C) humid greenhouse conditions. In April 1990, other seeds were put in an agar medium with nutrients and kept at 15°C.

Results

The flowering sequence of *Chusquea talamancensis, C. tomentosa* and *C. subtilis* is represented in Table 3. Isolated clumps of *Chusquea talamancensis* (Figures 4, 5) began to flower at the end of 1987 in the areas of Cerro Asunción and Cerro Cuericí. These plants died gradually without producing any seed. In October 1988, larger patches of this bamboo species flowered in the areas of Cerro Asunción, La Georgina, Villa Mills and Cerro Cuericí. Flower development took 3 months, anthesis occurred in the following dry season (March 1989), and fruit formation took about a year. Mature seeds were found in the dry season of 1990. At the beginning of the month of June 1990, the panicles were almost fruitless; fruit set had already occurred, but no seedlings were located. Seedlings up to 5 cm tall were observed in July 1990, in the rainy season. After flowering, the parent plants dried out and died.

The seeds sown under warm (22°C) greenhouse conditions germinated in April 1990 (Figure 5C), three months earlier than under natural conditions in the forest (mean temperature of 11.9°C; Blaser, 1987), and the seeds sown *in vitro* germinated at the same time as in the forest.

About 43.5% of the population of *Chusquea talamancensis* initiated flowering a year later, in October 1989. These clumps followed a similar flowering schedule as the plants that flowered a year earlier. In December 1991, the forest floor was covered with seedlings and one-year-old plantlets. Meanwhile, the whole parent population was in the process of senescence, except for a few isolated clumps which remained in vegetative condition; it is not known whether they flowered after 1991.

Six hundred and seven clumps of *Chusquea talamancensis* were surveyed at the end of 1989 in the CATIE plots. Half of them had inflorescences, half had infructescences (Table 4a). The survey carried out in March 1990 in the author's ecological plots resulted in a similar finding; out of a total of 447 clumps of *Chusquea talamancensis*, 0.7% began to flower in 1987, 55.7% in 1988, and 43.6% in 1989 (Table 4b). The phenological state of the caryopses was determined from 14 voucher specimens of *Chusquea talamancensis* sampled in March 1990. From a total of 140 caryopses, 25% were mature, while the majority (46%) were immature, and 29% were empty. The total seed production was estimated to be 3 - 4 kg/clump of bamboo.

There was a remarkable synchronism in the phenological sequence, even at distant locations such as Cerro Chirripó. M. Kappelle sampled specimens in anthesis in January 1989; in April 1989 the collected sample showed immature fruits. The event took place not only in the Eastern Cordillera de Talamanca (Atlantic side), but also on the Western (Pacific) side. H. van Velten sampled specimens at the valley of the Río Savegre that had incipient fruits in 1989.

Chusquea tomentosa (Figure 6) showed a pattern of flowering in the area of Cerro Abarca-Cerro Cuericí similar to that of *C. talamancensis:* in the first year isolated clumps flowered without producing seeds; a year later mass flowering was observed throughout the whole area. Sporadic flowering started in 1989, a year later than *Chusquea talamancensis*, but the flowering sequence took place earlier in the year (Table 3). The incipient flowers appeared

in August, anthesis occurred in December 1989, and incipient fruits were already present in March 1990. The flowering survey at the end of 1989 showed that 5% out of a total of 904 clumps of *Chusquea tomentosa* were flowering. In the author's ecological plots, 8% of *Chusquea tomentosa* clumps were in flower in March 1990, while in December 1991 almost all plants were flowering. Seedlings were observed in the study area in 1992 (G. Sáenz, pers. comm.). In the greenhouse in Switzerland, two plants of *Chusquea tomentosa* also flowered in 1991 and in 1992 respectively, but produced no seed and died thereafter (Figure 6C).

　　　Chusquea subtilis is less widely distributed in the study area than *C. talamancensis* and *C. tomentosa* and its phenology was not studied in detail. In December 1988, however, clumps at Villa Mills bore immature flowers in the primary forest and mature flowers in an open site (Table 3). In November 1989, the plants in the forest still had immature fruits whereas those in the open site already bore mature fruits, and seedlings were found beneath the senescent, almost leafless parent plants. The survey made in the forest in November 1989 showed that *Chusquea subtilis* had 80% of the clumps bearing fruits.

Discussion
Flowering cycle

　　　The flowering cycle of semelparous *Chusquea* species is equivalent to its entire life cycle (Figure 7). The zygote develops into a mature caryopsis within a year while still attached to the mother plant. After abscission and a brief dormancy period, the seed germinates with the first rains. The "seedling" refers to the stage of development following germination until acquiring the full complement of vegetative structures (McClure, 1966). A seedling lives for less than a month on the endosperm reserves and increases its assimilating surface with rapid leaf development. After the establishment of a rhizome axis, a bamboo plant enters the juvenile phase as it acquires a bushy habit with lignified culms, larger leaves and further rhizome development (McClure, 1966). In these bamboo species, there is seasonality in the sprouting of new culms. In the rainy season and under favourable growth conditions (enough light and nutrients, no grazing), culm diameter and rhizome branch diameter increase annually. In an optimal environment, early development of the plants is nearly exponential (Gadgil and Prasad, 1984). Development slows down as the clump approaches maturity. After mass flowering it may take about 10 years for the clump to produce culms of the same diameter as they were before flowering in some Japanese species (Ueda, 1960). McClure (1966) calculated 3 - 20 years as the time needed for the plant to attain mature stature, depending on genetic constitution and the nature of its environment. According to Campbell (1985) a period of 15 - 20 years may be necessary for the clump biomass to recover completely.

　　　The vegetative phase of *Chusquea talamancensis* and probably other *Chusquea* species in the Cordillera de Talamanca is estimated to be 30 - 35 years, based on data on culm size before flowering (Widmer, in press) and from observations by local people. A flowering period of 31 to 33 years was reported four times for *Chusquea abietifolia* Griseb. in the Blue Mountains of Jamaica. Seifriz (1950) described mass flowering in 1884 - 1885, 1918 -1919, and 1948 - 1949, and K. Amman (pers. comm., 1993) observed flowering in 1981. This interval is similar to the majority of tropical bamboos which show a periodicity of between 30 and 35 years (Liese, 1985).

　　　The generative phase begins with flower initiation and finishes with fruit fall, senescence, and death. Panicles are formed terminally on the subsidiary branches of a culm and are morphologically axillary to the main axis of the plant (Clark, 1989). At flower initiation the mother plant is still fairly vital, probably because the flower generally has a lower priority than the fruit in attracting assimilates (Ho, 1992). After fertilization the mother plant undergoes leaf loss (about 50% of the leaves are shed) and the culms and branches become yellowish

while the plant allocates vital energy resources to seed production. Assimilates are continually translocated to the fruits, which become irreversible storage sinks in terms of assimilate partitioning (Goldwin, 1992; Ho, 1992). The process of culm decay is hastened by increased insect (borers) and fungal attack on the parent plant, as observed on Asiatic bamboo species (Numata, 1970). At fruit formation, vegetative growth has ceased completely and the parent plants gradually dry out. The culms crack easily and the plant has about 5 - 10% of its foliage left. Prior to fruit abscission the only visible green part of the mother plant is the pedicel, linking the caryopsis to the rachis of the panicle.

Seasonality of reproduction by seed

Seasonality is not only observed in the vegetative development of a *Chusquea* bamboo in the montane oak forests, but also in the process of flowering. The flowering pattern of a single plant of *Chusquea talamancensis* follows the seasonal rainfall pattern. A single plant or a clump is defined as either a sexually derived individual, i.e. a genet, or a disconnected ramet resulting from self cloning (sensu Urbanska, 1992).

The diminished culm production or the reduced diameter of new culms in the preceding rainy season are signals for future flowering of a bamboo plant. This has also been observed in Asiatic bamboo species (Deogun, 1937; Ueda, 1960). Flower initiation begins in the late rainy season (October) and the spikelets develop until the beginning of the next dry season (December). The culms of a clump do not always flower in synchrony; some plants have culms in two different phenological states. Flower formation lasts for about three months until the flower has developed the generative parts. Flowers are hermaphroditic and monomorph; dichogamy was not observed. As another example, flowers of *Ochlandra travancorica* (Bedd.) are hemaphroditic and typically dichogamous and protogynous (Venkatesh, 1984). Anthesis occurs simultaneously in all flowering clumps during the dry season (January-February). Fertilization takes place within a very short time and incipient fruits are soon found in the spikelets. Fruit formation lasts for about a year until the fruits reach maturity, which is a long time compared to other bamboo species. The low temperature and the daily short time of direct radiation in the montane cloud forests may be the principal factors that limit physiological processes such as assimilation, respiration, or, in the case of flowering, translocation of nutrients from the mother plant to the fruits. Fruit maturation is attained in the dry season. A desiccated fully mature grain of *Chusquea talamancensis* is built with a resistant seed coat as wheat and barley grains. The caryopsis has the appearance of a rice grain with a furrow which runs along the ventral side and the embryo is at the base of the caryopsis on the opposite dorsal side (Figure 3C). Germination takes place with the beginning of the rainy season; the onset of rain may be the dormancy-breaking mechanism. Dormancy may be enforced (Harper, 1997) because the seeds collected in January in the forest and sown under warm and humid greenhouse conditions germinated three months earlier than in the forest. Besides, the seeds sown under cooler climate chamber conditions germinated almost simultaneously with those in the forest. In the oak forests of the Cordillera de Talamanca *Chusquea talamancensis* needs two years from the initiation of flowering until the seeds germinate and the forest floor is covered with seedlings. Similar observations were made by Tong-Pei (1985) in China with the montane species *Fargesia nitida* (Mitford) Keng.

Predation and seed dispersal

Predation by insect larvae occurs in the spikelets of *Chusquea talamancensis* and *C. tomentosa* while the flowers are formed. The larvae grow to the size of the palea, feed on the reproductive organs and develop to a pupa. The adult insects found in the spikelets of herbarium specimens are likely to belong to a phytophagous group of the parasitoid genus *Aprostocetus* (Chalcidoideae: Tetrastichinae) (J. LaSalle, Natural History Museum, London,

1994).

At the time of fruit maturation and fruit fall, the bamboos were actively visited by birds. Apart from parrots, the nomadic species *Acantidops bairdii* (Emberizidae), endemic to Costa Rica, increased its population while feeding on *Chusquea* seeds (J. Sánchez, Museo Nacional de Costa Rica, 1990). The rodent population must also have increased, as it has been observed for other bamboo species (Janzen, 1976).

Birds and rodents may also be passive dispersal agents when caryopses that have been eaten are not digested but pass in the feces. In addition, spikelets are externally scabrous and adhesive and bear an awn on the fertile and sterile lemmas (Figure 3), which enables the fruit to attach to the fur or plumage of animals and may thus be dispersed over a potentially large area ("armed seeds," Radosevich and Holt, 1984).

Flowering at Population Level

Depending on the population size and its genetic diversity, the time of flowering at population level extends over more than 3 years. Mass flowering of other bamboo species has been described as beginning at one site and then extending over the whole area within a period of 2 - 4 years (Seifriz, 1920; Deogun, 1937; Dwiwedi, 1988).

There is a temporal sequence of flowering at the population level in *Chusquea talamancensis* where groups of plants flower in successive years. These cohorts have different sizes and are patchily distributed over the whole area. According to Troup (1921 in Huberman, 1959), flowering follows a sequence of at least three phases at the population level: preliminary sporadic flowering, mass flowering, and final sporadic flowering. Filgueiras and Pereira (1988) observed in flowering populations of *Actinocladum verticillatum* (Nees) McClure ex Soderstrom that in the first year a few clumps flowered erratically, and in the second year most of the population flowered while some clumps remained sterile. The present work suggests that the flowering in *Chusquea talamancensis* includes three phases. In the first year, some isolated plants flower but bear no seed, then two mass-flowering cohorts flower in subsequent years (each about 49% of the population) with profuse seed production. A few isolated plants remain in vegetative condition or may flower out of phase.

Mass flowering of *Chusquea tomentosa* seems to follow the same pattern. At least three phases can be distinguished: 1) isolated plants flowering in the first year without progeny, 2) a cohort comprising 5 - 8% of the population, and 3) a mass flowering cohort. It must be said that the area studied by the author corresponds to the uppermost limit of distribution for this bamboo. *Chusquea tomentosa* populations at lower elevations (La Esperanza del Guarco, Trinidad de Dota) were already in full flower when the event was just starting at higher elevations (Cuericí), indicating that the flowering time may also be dependent on the local environmental conditions (Widmer, 1994).

Chusquea subtilis shows three cohorts; the largest one consists of plants with mass flowering, whereas two smaller ones form flowers before and after the mass flowering cohort. In this bamboo species it was observed that the rate and duration of fruit growth and maturation are affected by the prevailing environmental conditions as described by Duffus (1992), being shorter in open areas.

Seedlings of all the *Chusquea* species studied here were only observed after mass flowering, suggesting that reproductive success depends on cross-pollination. Neither the isolated or sporadic flowering clumps in the forest, nor the transplanted ones in the greenhouse (which flowered in successive years), produced seeds. The reproductive mechanism is probably species-specific, since self-compatibility was shown for other bamboo species such as *Sasa nipponica* and *S. senanensis* (Nishiwaki and Konno, 1990) and *Ochlandra travancorica* (Venkatesh, 1984). Nevertheless, it is obvious that the genetic variability of a population can

only be maintained through outbreeding, and the best opportunity for the *Chusquea* species of the Cordillera de Talamanca is when mass flowering occurs.

Acknowledgements

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NICARAGUA

Caribbean Sea

COSTA RICA

STUDY SITE

San José   Limón

Puntarenas

PANAMA

Pacific Ocean

9°35'16"

Cerro Asunción

Cerro Abarca

CORDILLERA DE TALAMANCA

Cerros Cuerici

N

Villa Mills

La Georgina

Siberia

PROVINCIA

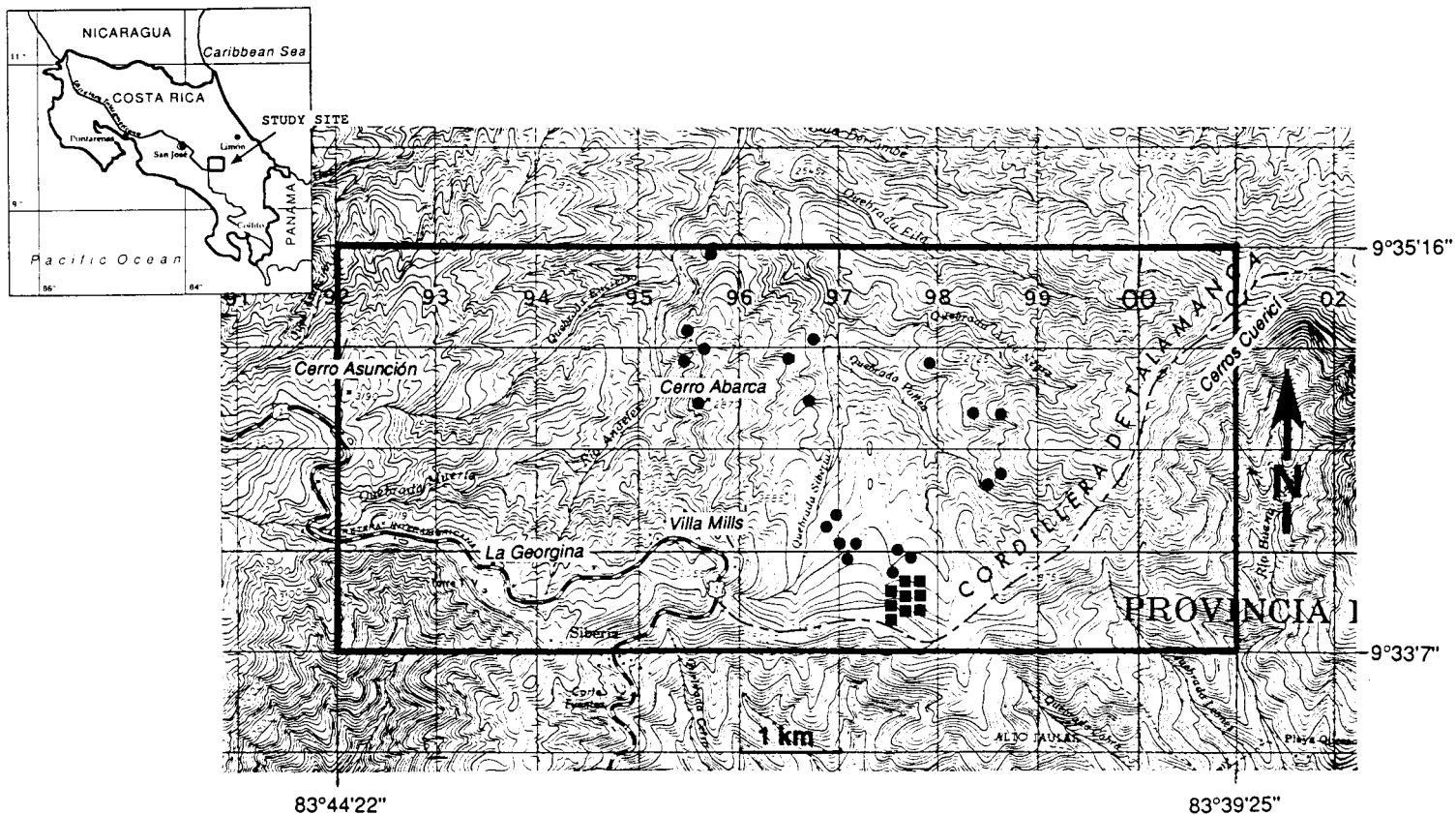9°33'7"

1 km

ALTO JAULAR

83°44'22"

83°39'25"

Figure 1. The area of phenological observations in the Cordillera de Talamanca, Costa Rica. (Topographic map reproduced with the permission of the Instituto Geográfico Nacional, San José, Costa Rica; November 3, 1992.). Dots: ecological plots; squares: silvicultural plots.
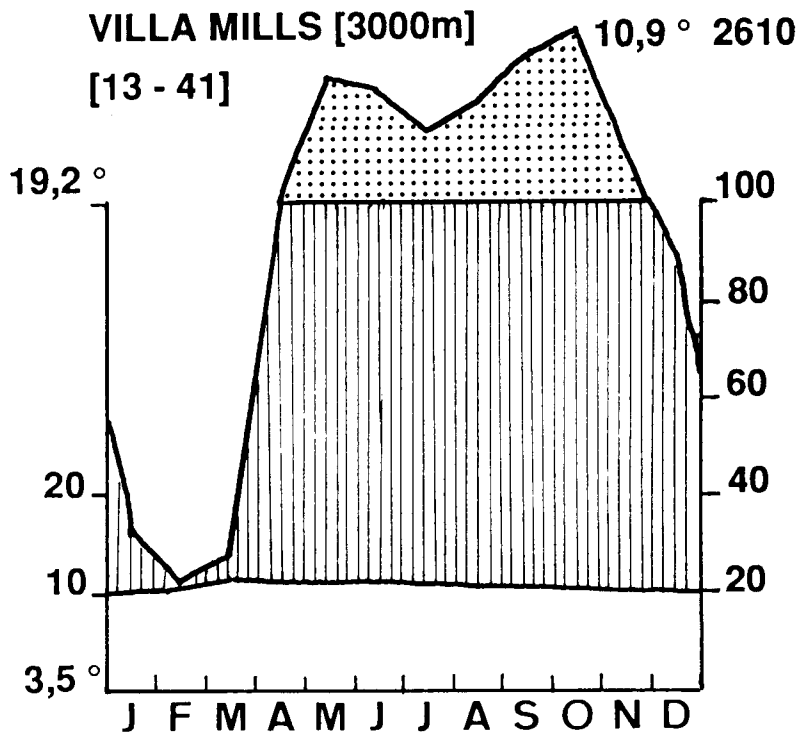
Figure 2. Climate diagram of Villa Mills (Costa Rica) showing the seasonal rainfall regime. Adapted from Blaser (1987).
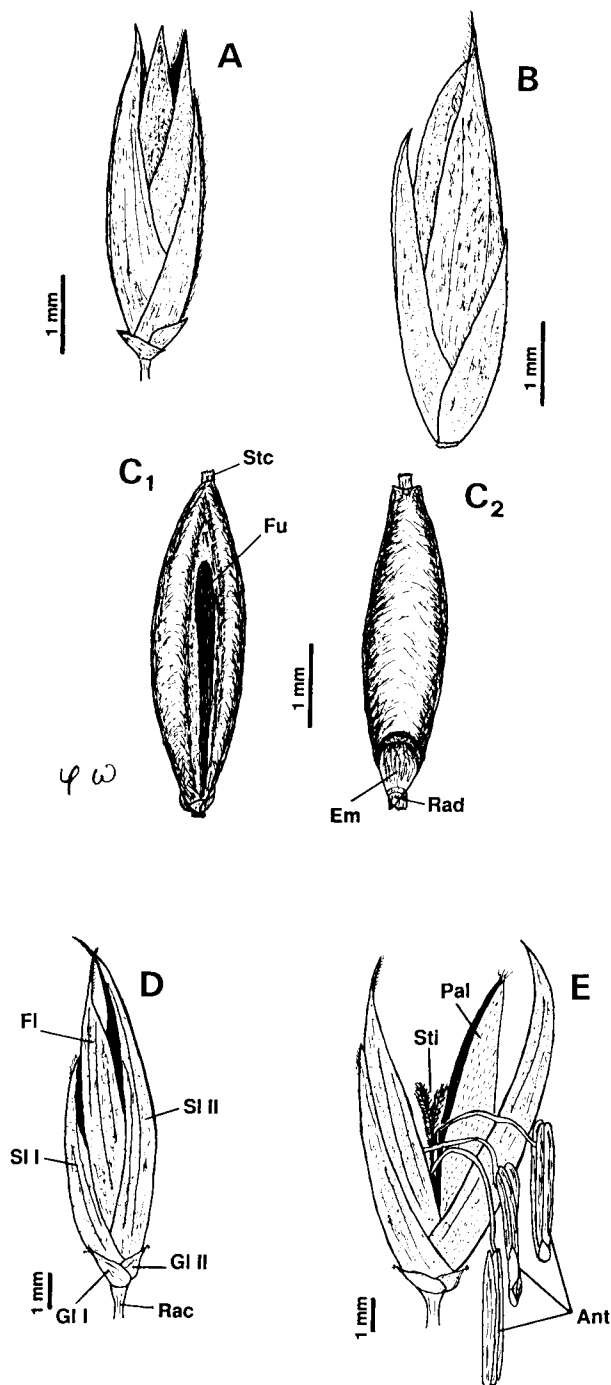
Figure 3. *Chusquea talamancensis.* A. spikelet (1120); B. caryopsis; C1,2. anterior (1) and posterior (2) view of a caryopsis without lemmas and palea (1112). *Chusquea tomentosa.* D. spikelet; E. open flower (1053). Ant: anthers, E: embryo, Fl; fertile lemma, Fu: furrow, GlI: glume I, GlII: glume II, Pal: palea, Rac: rachilla, Rad: radicle, SlI: sterile lemma I, SlII: sterile lemma II, Stc: stylar column, Sti: stigma. Drawn by the author.
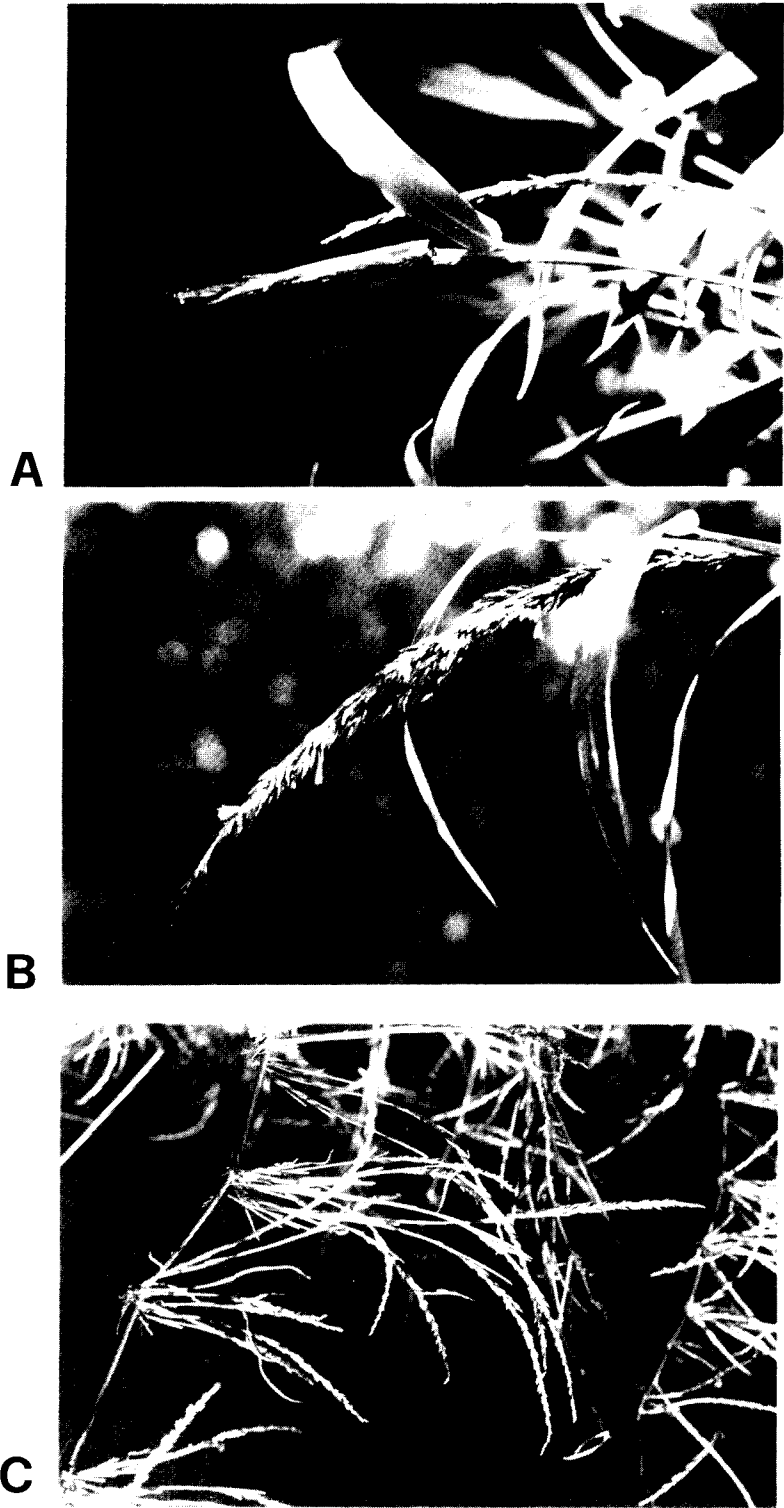
Figure 4. *Chusquea talamancensis.* Panicles A. with incipient flowers, B. with open flowers, C. with fruits on a senescent plant.
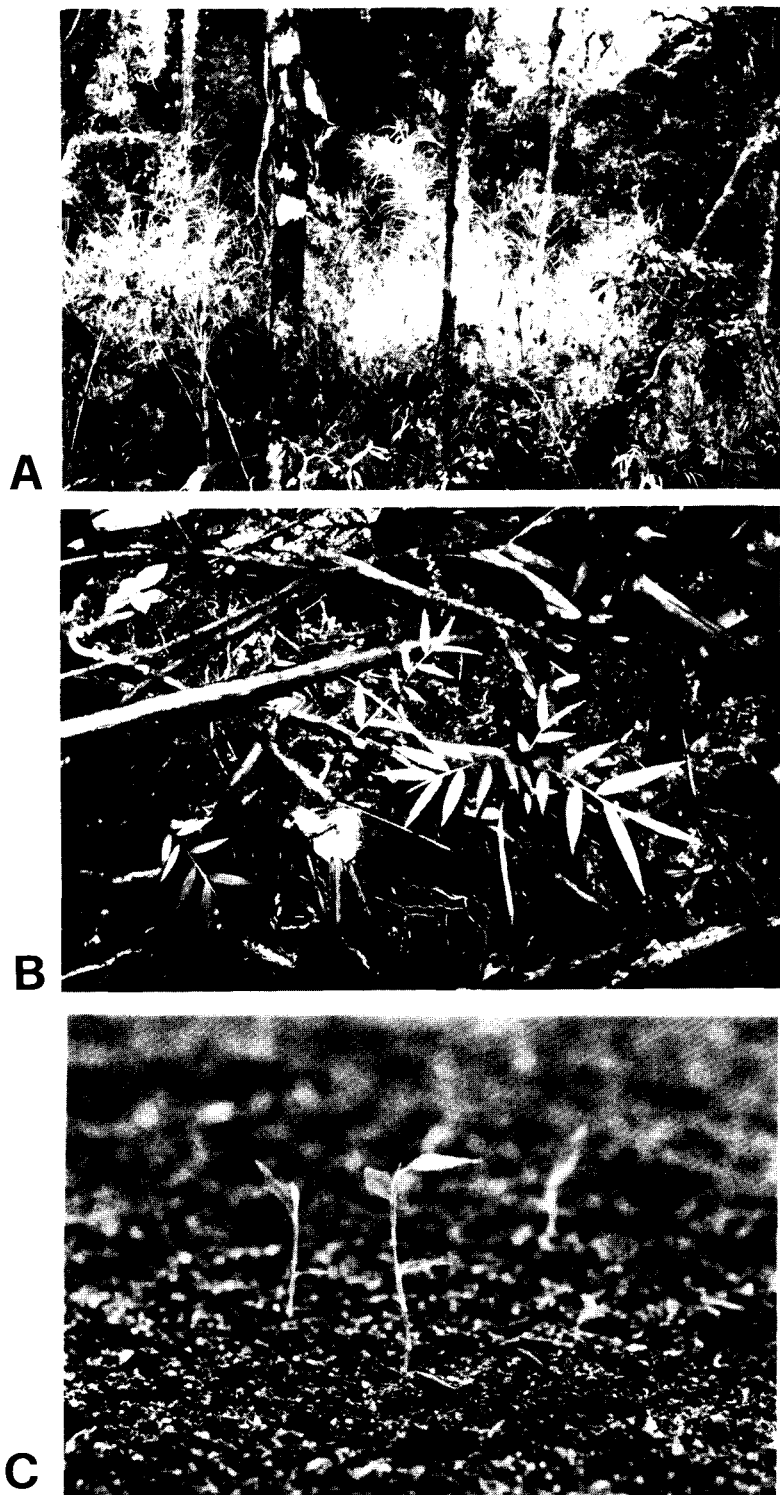
Figure 5. *Chusquea talamancensis.* A. Forest understory with plants in the phase of fruit fall and senescence. B. Seedlings on the forest floor (Photo: M. Kappelle). C. Seedlings in a germination bed in the greenhouse at CATIE.
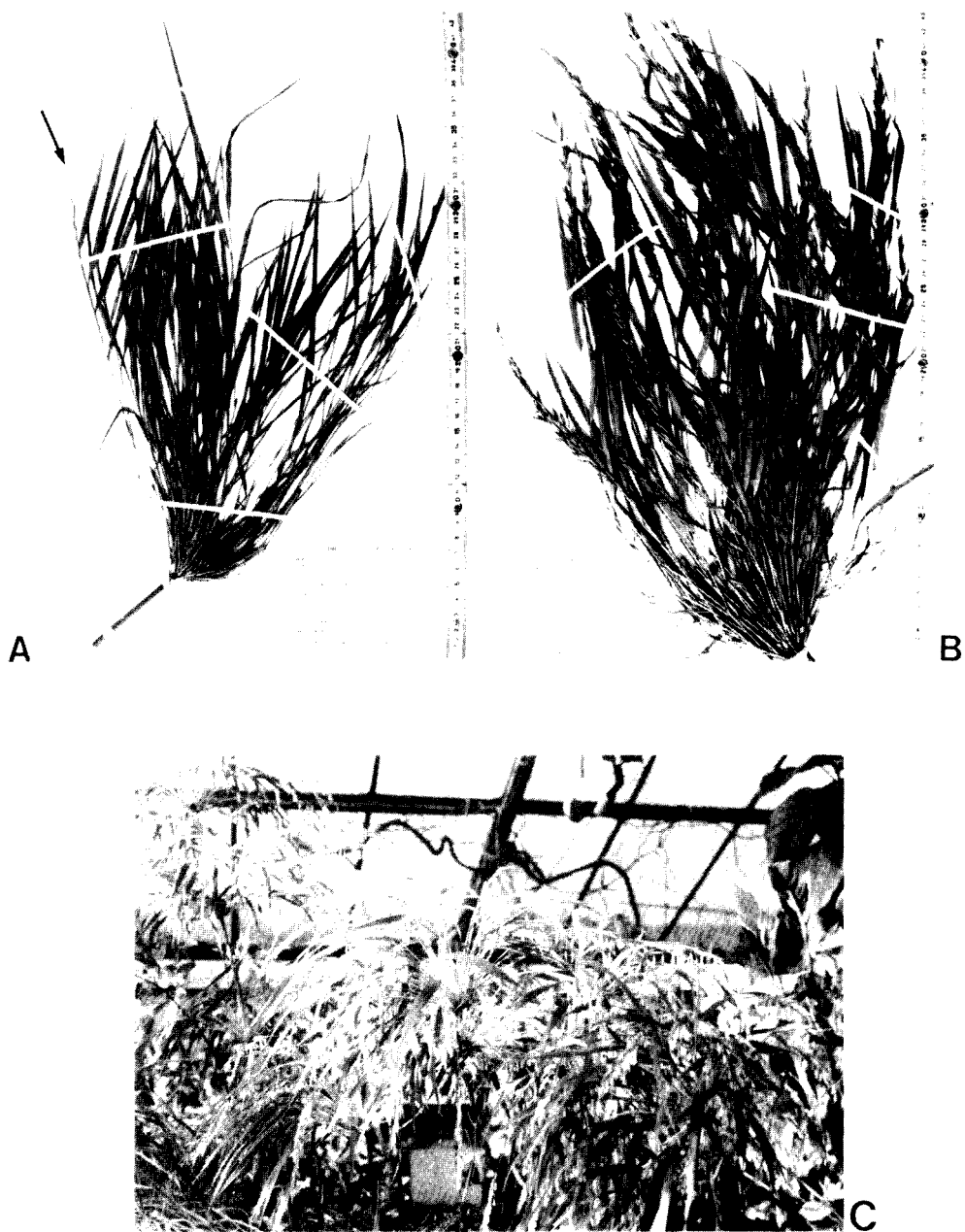
Figure 6. *Chusquea tomentosa.* A. Culm complement, panicles with incipient flowers (500). B. Culm complement, panicles with mature flowers (502). C. Flowering plant in the greenhouse in Switzerland.

ZYGOTE ■

postzygotic development   1 year

RIPE FRUIT ■

domancy   1-2 months

GERMINATION ■

living on endosperm reserves   1 month

SEEDLING ■

juvenile development   3 years*

PLANTLET ■

development of a functional rhizome 5 years*

ADULT ■

vegetative phase   25-30 years*

FLOWER INITIATION

flower formation   3-4 months

ANTHESIS ■   2 months
pollination

FERTILIZATION ■

fruit formation
                                 1 year
degradation

FIRST FRUIT SET ■

fruit
senescence   3 months

LAST FRUIT SET ■
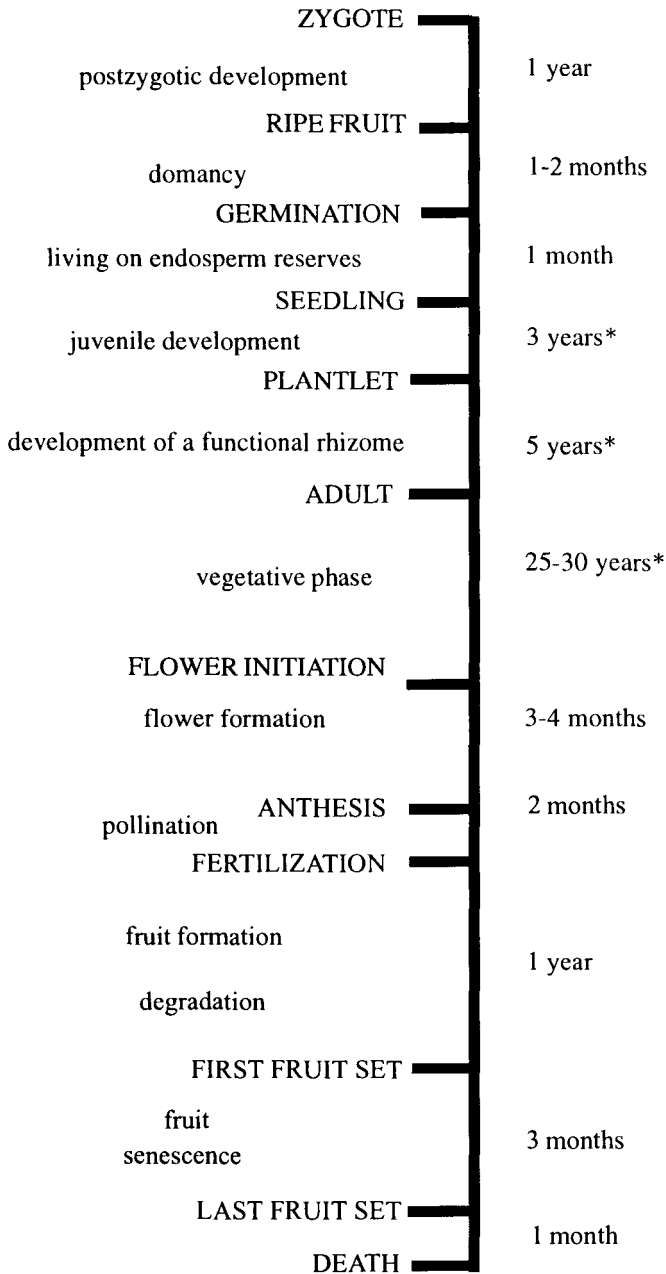   1 month
DEATH ■

Figure 7. Life cycle of *Chusquea* as represented by *C. talamancensis* based upon phenological observations. Adapted from Harper (1977). *assumptions.

Table 1. List of voucher specimens of *Chusquea* species

No.	Date	Site*	Altitude (m.a.s.l.)	Phenological stage(duplicates)	Herbarium
Chusquea talamancensis					
1099	24.10.87	Cerro Asunción (1 km N CIA)	3,000	inmature flower	CR/Z+ZT(2)
520	10.08.88	Cerros Cuericí (Plot 5E3)	3,010	vain flower	CR/CATIE-SBN/Z+ZT(3)
521	11.08.88	Cerros Cuericí (Plot 4C5)	2,980	vain flower	CR/Z+ZT(5)
539	09.12.88	Villa Mills ("El Sitio")	2,600	immature flower	Z+ZT
523	25.10.89	Villa Mills (Pilot Area CATIE)	2,700	incipient flower	CR/Z+ZT(2)
518	26.10.89	Cerro Abarca (Plot Faja CATIE)	2,800	incipient flower	CR/Z+ZT(2)
522	26.10.89	On the track to Cerro Abarca	2,800	immature fruit	CATIE-SBN/CR/Z+ZT
1134	09.11.89	Cerros Cuericí (Plot AN3 CATIE)	2,830	incipient flower	Z+ZT
1136	09.11.89	Cerros Cuericí (Plot Puma CATIE)	2,830	immature fruit	Z+ZT
1138	09.11.89	Cerros Cuericí (Plot Puma CATIE)	2,830	immature fruit	Z+ZT
1140	15.11.89	Villa Mills (Plot PlacIII CATIE)	2,720	immature fruit	Z+ZT
1120	07.03.90	Cerros Cuericí (Plot 4E1)	3,000	mature flower	Z+ZT
1112	07.03.90	Cerros Cuericí (Plot 5C2)	2,990	mature fruit	Z+ZT
1113	07.03.90	Cerros Cuericí (Plot 5E6)	3,060	mature fruit	Z+ZT
1110	08.03.90	Cerros Cuericí (Plot 4C1)	2,970	mature flower	Z+ZT
1111	08.03.90	Cerros Cuericí (Plot 4C14)	2,980	mature fruit	Z+ZT
1131	09.03.90	Cerros Cuericí (Plot 4D5)	2,900	mature fruit	Z+ZT
524	23.03.90	La Georgina (1 km SW CIA)	3,100	vegetative	CR/CATIE-SBN/Z+ZT(3)
550	03.06.90	On the track to Cerros Cuericí	3,000	vegetative	CATIE-SBN/Z+ZT(4)
1107	11.12.90	On the track to Cerros Cuericí	3,000	seedlings	Z+ZT
1108	11.12.91	On the track to Cerros Cuericí	3,000	seedlings	Z+ZT
Chusquea tomentosa					
1020	04.05.89	By the road to Cerros Cuericí	2,850	vain flowers	CR(2)/Z+ZT(6)
500	19.08.89	Villa Mills (by the quebrada Voltea)	2,680	incipient flower	ISC/CR/Z+ZT(3)
501	10.11.89	Villa Mills (Pilot Area CATIE)	2,700	mature flower	ISC/CR/Z+ZT(2)
502	15.11.89	Cerros Cuericí (Plot AN2 CATIE)	2,710	immature fruit	ISC/CR/Z+ZT
1050	09.12.89	Cerros Cuericí (Plot Puma CATIE)	2,800	mature flower	CR/Z+ZT(3)
1053	11.12.89	On the track to Cerros Cuericí	3,000	mature flower	CR/Z+ZT
1027	06.03.90	Cerro Abarca (Plot 6D1)	2,800	incipient fruit	Z+ZT
1033	07.03.90	Cerros Cuericí (Plot 5C13)	3,020	incipient fruit	Z+ZT
1023	07.03.90	Cerros Cuericí (Plot 5C3)	3,010	vegetative	Z+ZT
Chusquea subtilis					
527	09.12.88	Villa Mills (Pilot Area CATIE)	2,700	inmature flower	CATIE-SBN/Z+ZT/CR
508	09.12.88	Villa Mills ("El Sitio")	2,580	mature flower	ISC/CR/CATIE-SBN/Z+ZT(4)
993	15.12.88	Cerros Cuericí (Plot 5C5)	3,010	mature flower	Z+ZT
514	15.11.89	Villa Mills ("El Sitio")	2,580	mature fruit	ISC/CR/CATIE-SBN/Z+ZT
994	15.11.89	Villa Mills ("El Sitio")	2,580	seedlings	Z+ZT

* There are two kinds of plots: 1) those of the Silviculture of Natural Forests Project with the abbreviation CATIE (Centro Agronómico Tropical de Investigación y Enseñanza, and 2) those from the ecological research of the author with numbers and letters (e.g. 5E3).

CIA: Carretera Interamericana (Panamerican Highway)

Herbaria: CATIE-SBN: Herbarium of the Silviculture of Natural Forests Project, CR: Herbario Nacional de Costa Rica, ISC: Herbarium of Iowa State University, Z+ZT: Zürich Herbarium. In brackets number of duplicates.

Table 2. Differential characteristics of flowers and fruits in *Chusquea talamancensis,*
C. tomentosa, and C. subtilis used for phenological classification in the field.

Species & state	Glume	Sterile lemma	Fertile lemma
C. talamancensis flower fruit	violet (or green) dry	violet (or green) dry	green green
C. tomentosa flower fruit	dry (or violet) dry	violet dry	green green
C. subtilis flower fruit	green dry	green dry	green green

Season / Chusquea	Event %	rainy season	dry season	rainy season	dry season	rainy season	dry season	rainy season	dry season	rainy season	dry season	rainy season
C. talamancensis												
1987: Isolated plants	0.7											
1988: Mass flowering	55.7											
1989: Mass flowering	43.6											
C. tomentosa												
1987: Isolated plants	0.1*											
1989: Sporadic flowering	8.0											
1990: Mass flowering	91.9*											
C. subtilis												
1988: Mass flowering (o.s.)	-											
1988: Mass flowering (f.c.)	-											

Months	J A S O N D	J F M A M J J A S O N D	J F M A M J J A S O N D	J F M A M J J A S O N D	J F M A M J J A S O N D	J F M A M J J A S
Year	1 9 8 7	1 9 8 8	1 9 8 9	1 9 9 0	1 9 9 1	1 9 9 2

LEGEND

· · · · · ·	Flower formation = leafy branches with terminal inflorescence
————	Anthesis / leaffall and yellowing of culms
— · — ·	Fruit formation / senescence of mother plant
— — · — ·	Fruit maturation and fruitfall / death of mother plant
———▶	Germination => seedlings (new generation)
— — +	Degradation and death of plants / without seeds
?	No information
*	Estimation

Note: Years on the first column stand for the year when flowering started.
Clumps of *C. subtilis* were all flowering, in the open site (o.s.) and under forest canopy (f.c.).

Table 3. Phenological table with the flowering process of *Chusquea talamancensis, C. tomentosa,* and *C. subtilis* in the area Cerro Asunción to Cerros Cuerici from 1987 to 1992.

a.)

Species Phen. state	*Chusquea talamancensis*		*Chusquea tomentosa*		*Chusquea subtilis*	
	No. clumps	%	No. clumps	%	No. clumps	%
Vegetative	13	2	858	95	1	10
Flower (Flo)	297	49	46	5	1	10
Fruit (Fru)	297	49	0	0	8	80
Total clumps	607	100	904	100	10	100
Total clumps Flo or Fru	594	98	46	5	9	90

b.)

Species Flowering year	*Chusquea talamancensis*		*Chusquea tomentosa*	
	No. clumps	%	No. clumps	%
1987	3	0.7	0	0
1988	249	55.7	0	0
1989	195	43.6	19	8
Total clumps	447	100	246	100
Total clumps Flo or Fru	447	100	19	8

Table 4. a. Phenological states of clumps of *Chusquea talamancensis, C. tomentosa* and *C. subtilis* in October/November 1989 (data from CATIE plots); b. Proportion of flowering plants in a temporal sequence from 1987 to 1989 (data from plots of the author's ecological study).

Chris Stapleton*: **Form and Function in the Bamboo Rhizome**

Abstract

Bamboo rhizomes are taxonomically and horticulturally very important, but the terminology used to describe them has often been confused or imprecise. Two major forms of rhizome prevail. The terms pachymorph and leptomorph were favoured by McClure and their use is recommended, rather than the terms sympodial and monopodial. The separation of terminology describing culm growth from that describing rhizome form is considered beneficial, and the term amphipodial is considered to be potentially misleading and undesirable. The possible functions of two particular forms of rhizome are suggested. The long hollow necks of the pachymorph rhizomes in certain *Yushania* species may be an adaptation to seasonally waterlogged sites, and the metamorph II axis seen in *Vietnamosasa* species may be related to a high incidence of fires in their natural habitats. The distribution patterns of bamboos with several different rhizome forms in the Himalayas are described in relation to precipitation, and various functions of the two major rhizome forms are discussed.

Introduction

Although they are not the most accessible parts of the plant, rhizomes are particularly important in the bamboos, both ecologically and horticulturally. They control when the culms develop and how they spread, and they also dictate vegetative propagation techniques. Taxonomists have not always considered rhizome forms to be important in bamboo classification. They continue to this day to disagree upon their value, and whether they should be used to separate subtribes. However, it is now accepted that rhizome form, in conjunction with other characters, is very useful for the separation of bamboo genera. Nevertheless, there is a great deal of confusion at the present time as to which terminology is appropriate for bamboos with particular forms of rhizomes, and how the different terminologies relate. These misunderstandings can cause difficulties even at the highest levels of study. Watanabe et al. (1994), in a cladistic analysis of chloroplast DNA from Asian bamboo genera related morphological variation to DNA restriction site mutations. They mistakenly thought they could not demonstrate a clear distinction between the DNA of genera with monopodial and sympodial rhizomes, as they did not apply the terms accurately, incorrectly attributing *Melocanna* Trin., *Thyrsostachys* Gamble, and *Yushania* Keng f. with possession of monopodial rhizomes. It is understandable that in this state of confusion many horticulturalists are happy to call them simply clumpers or runners.

McClure (1966) gave a very detailed and perceptive description of the bamboo rhizome. He separated two distinct forms, now most commonly known as the pachymorph (or sympodial) form, and the leptomorph (or monopodial) form. He generously attributed this distinction to the Rivières (1878), although they had been describing the clumping habit (caespitose or spreading) rather than the rhizome itself. McClure was in fact the first to describe the two different forms of rhizome, applying the terms sympodial and monopodial in his first publication (McClure, 1925).

This distinction is well understood by most of those who have any experience of handling bamboos. However, several terms have been coined for these two forms of rhizome, and this has caused confusion. The problem is compounded when ambiguous terminology is introduced, especially the term amphipodial, which blurs the distinction unnecessarily. McClure (1966) gave an illustration of *Chusquea fendleri* Munro, in which leptomorph rhizomes produce very swollen tillering culm bases, some having marked horizontal growth, and appearing very similar to pachymorph rhizomes. The rhizomes of such bamboos have been described as

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amphimorph or amphipodial. The use of these terms may be rather misleading, however. They clearly imply possession of both leptomorph and pachymorph rhizomes in a single plant, but so much depends upon how a rhizome is defined. In a segmented plant such as a bamboo, with all axes based simply upon nodes and internodes, it is difficult to produce a watertight definition of a rhizome or any other class of axis. When does a rooting culm base or branch base become a rhizome? In a plant such as *Chusquea fendleri* in which the mature leptomorph rhizome axes are so well differentiated from all other axes, it could be asked whether it is correct to describe any other part of the plant as rhizome as well.

I personally think that the principal cause of confusion in the description of bamboo rhizomes is the lack of separation of terminology that is applicable strictly to the rhizome from terminology designed to cover culm or clump habit. There has too often been an attempt to describe both with a single term. It is much more satisfactory if descriptions of bamboos include clear-cut simple terms for the rhizomes below the ground, and a further note of how the culms arise above the ground, in which case potentially misleading terms such as amphimorph and amphipodial are not necessary. McClure (1973) followed this practice in his precise descriptions of American bamboos.

Rhizome Terminology

The classification of bamboo rhizomes may appear to have become very complicated, but several terms are clearly synonymous. Essentially, bamboo rhizomes vary only in how they branch, and in the appearance of their constituent internodes. There are two clear-cut forms of branching. Those rhizomes that branch rarely and can stay under ground with indefinite apical growth have monopodial branching (Fig. 1). Those rhizomes that rise up to form a culm every year and cannot stay under the ground must branch repeatedly. They could form a structure known as a sympodium (Fig. 2), where an axis (the rhizome) is actually composed of many sections of separate axes that have branched repeatedly. This is why such rhizomes are said to have sympodial branching. In fact a single axis as portrayed in Fig. 2 is rarely produced, and a much more complex ramification is usual, without any clearly defined sympodium, so that the term sympodial is being applied rather loosely. The terms monopodial and sympodial can also cause confusion as they seem at first sight to be applicable to the culms rather than the rhizomes. Lin (1961) unfortunately misused them in this way, which may be why McClure decided not to continue using these terms himself.

The growth of the rhizome can also be described as determinate or indeterminate, and this distinction reflects an important difference in the longevity of their apical meristems, but these terms are now rarely used for the rhizome. Determinate is equivalent to sympodial, and indeterminate to monopodial.

There are also two forms of rhizome appearance. The internodes are usually either thickened somewhere along the rhizome (pachymorph) or uniformly thin (leptomorph), relative to the culm. Fortunately, monopodial rhizomes are always leptomorph, and sympodial rhizomes are always pachymorph. Thus, all these terms are synonymous: monopodial = leptomorph = indeterminate, and sympodial = pachymorph = determinate.

McClure in his final glossary (1973) used the terms pachymorph and leptomorph in preference to all other terminology, but in the Chinese taxonomic literature the terms monopodial, sympodial, and amphipodial reign supreme. In popular accounts a variety of terminologies are applied, and in one account (*Bamboos of China*: Wang & Shen, 1987) their use seems difficult to understand at all unless the captions to the figures have become juxtaposed.

The term metamorph (changing form), introduced by McClure (1966; 1973), was never applied to the rhizome system as a whole, but was used to describe short sections of axes that

came between the rhizome and the culm, in effect culm bases. I do not believe that McClure would ever have applied the term to the entire rhizome system of the plant as applied by Lin (1978) or in the book *Chinese Bamboos* (Chen & Chia, 1988), and it should be considered an optional accessory refinement rather than a fundamental category. The metamorph I axis of McClure (1966) encompasses tillering of culm bases in both leptomorph and pachymorph rhizomes. The metamorph II axis is apparently peculiar to the pachymorph rhizomes of the genus *Vietnamosasa* T.Q. Nguyen, and I suggest below that this may reflect an unusual adaptation of the rhizome to a particular habitat.

The term amphipodial is widely used for bamboos that tiller from the base of culms arising from leptomorph rhizomes (Fig.3). As stated before, the term amphipodial implies possession of both monopodial and sympodial rhizomes. However, the tillering culm bases are not usually as thickened as a normal pachymorph rhizome, and they do not usually have a pronounced horizontal growth habit (diageotropic growth). Given the disparity between culm and leptomorph rhizome in such plants it is hard to consider these culm bases to be rhizome at all. Are all swollen branch bases with aerial roots from the mid-culm region of bamboos also to be classed as rhizomes?

Pachymorph rhizomes are thickened at some point, but they may have long thin necks (long-necked pachymorph), which usually bear no roots. These long necks have also been termed pseudowhips (Keng, 1982) and rhizoids (Wen, 1985). In some bamboos with long-necked pachymorph rhizomes, such as *Melocanna baccifera* Kurz and *Guadua angustifolia* Kunth, the neck length is fairly uniform. In others, such as *Yushania* species, the length of the neck varies greatly. The thickened portion of the rhizome has several buds, from which new rhizomes can grow. In *Yushania* new rhizomes that arise from buds at nodes lower down and closer to the neck of the parent rhizome will themselves have long necks. New rhizomes that arise from buds at nodes higher up the parent rhizome and closer to the culm have progressively shorter necks, the highest nodes giving the shortest rhizomes. In this way each rhizome gives birth to an array of daughter rhizomes with different neck lengths (see Fig. 4).

Culm and Clump Terminology

How the culms arise from the rhizome is also very important. In many cases the actual rhizomes of a bamboo are not investigated and a description of a bamboo is based upon what can be seen above the ground. In many cases it is not possible to deduce what the rhizome is like from the above-ground appearance. Similarly it may not be possible to predict how a bamboo will appear above the ground from the form of rhizome alone. Therefore a separate description is very useful for the culm or clumping habit, and fortunately the terminology for this is not as complicated as rhizome terminology.

The culms of a bamboo may arise in a consistently well-separated fashion from vigorous leptomorph rhizomes. In such a pattern of growth we can simply call the culms diffuse, arising singly, or isolated. The culms of bamboos with pachymorph rhizomes without long necks arise in a clump and are caespitose (strictly unicaespitose, alternative spellings cespitose, unicespitose, etc.), and always arise together in a clump. In bamboos with consistently long-necked pachymorph rhizomes, the culms may also arise singly in an isolated fashion, as in *Melocanna baccifera*. In bamboos in which the neck length varies, such as species of *Yushania*, a series of small separate clumps is produced. Such culms are pluricaespitose (also sometimes called multicaespitose or compound-caespitose). The culms of many bamboos with leptomorph rhizomes will often tiller at the base giving small separated clumps of culms. These are indistinguishable from the small separated clumps of culms arising from bamboos with long-necked pachymorph rhizomes, and their culms can also be called pluricaespitose. It is felt that 'rhizomes leptomorph; culms pluricaespitose' is a better way to describe these bamboos

than referring to their rhizomes as amphipodial.

The rhizomes and culms of some bamboos are well known for their different behaviour under different environmental conditions, and in juvenile and mature stages of growth. This usually applies to those bamboos that have leptomorph rhizomes when they are mature and growing vigorously. They can at times produce tillering clumps of culms with no real rhizome development. This can easily cause confusion in young plants or in plants growing away from their natural habitat. This variation in habit is one argument against the use of the term amphipodial. It leads to great overlap between the terms monopodial and amphipodial in the bamboos with leptomorph rhizomes at maturity, making the terms very difficult to define accurately or consistently.

Thus it seems accurate and quite adequate in presently known bamboos to describe the rhizome and culm habit of a bamboo according to whether the mature rhizomes are thickened (pachymorph) or uniformly thin (leptomorph); if thickened then either short or long (with or without elongated necks); and whether the culms arise singly (diffuse), in one large clump (unicaespitose), or in many small clumps (pluricaespitose). Combinations of these characteristics can be used in cases where they are variable. Leptomorph and pachymorph seem more appropriate than monopodial and sympodial, and amphipodial or amphimorph seem to be rather ambiguous and potentially misleading. As it is now becoming customary in definitions of bamboo rhizome terminology to give one's own preferred names for the four classic illustrations (But et al., 1984; Wen, 1985; Chen & Chia, 1988), I give my own interpretations of these in Fig. 5. This terminology will be followed in Kew's World Grasses Database, and in morphological and cladistic analyses undertaken at Kew.

Function of Different Rhizome and Clump Forms

The rhizome is obviously a crucial component of the bamboo plant, and it clearly has several different functions. The balance between these functions can be related to different habitats under which bamboos with different classes of rhizome grow, and a few interesting forms of rhizome development can probably be attributed to adaptation to particular environments.

In *Yushania microphylla* (Munro) R.B. Majumdar the elongated rhizome necks are completely hollow, even at the nodes, forming long uninterrupted tubes, and this may be related to the seasonally waterlogged sites in which this species is usually found. Hollow rhizomes may have developed from solid rhizomes, as an adaptation allowing transport of air to culms growing in wetter locations, or just to allow the rhizomes to grow further through soft soil. On the other hand, it may be that solid rhizomes have evolved from weaker, hollow rhizomes, in order to break through drier soil. McClure (1973) described small hollow rhizome canals in *Arundinaria gigantea* (Walter) Muhlenberg, which also often grows in seasonally waterlogged conditions.

The axes of *Vietnamosasa* species described as metamorph II by McClure (1966) are also quite distinctive. At first sight it seems as though the elongated neck has been placed at the wrong end of the rhizome. I suspect that the metamorph II axis between the rhizome and the shoots may be an adaptation to fire. All the collections that I have seen have suffered from fire-damage, coming from seasonally dry areas in Vietnam and Thailand, such as the area through which McClure travelled in 1953. It may seem surprising for a plant which is generally considered to require abundant water to be adapted to a fire-climax environment, but one form of bamboo fire-adaptation has already been described (Soderstrom, 1981), in the South American genus *Actinocladum* Soderstrom. In *Vietnamosasa* the metamorph II axis would ensure that the real rhizome remains deeply buried during fires, while still allowing rapid new growth of shoots, despite the variation in intensity and depth of soil-penetration of the

fire. The axis slants through the soil and bears many buds. It can produce new tillering culms and rhizomes from its new apex when all above-ground parts of the plant are burnt away. It will always have new buds just below the level of penetration of the fire, so that new shoots can compete well with other vegetation immediately. Slanting of the metamorph axis would reduce apical dominance and allow several shoots to grow at once.

It is not quite so easy to postulate why leptomorph and pachymorph rhizomes have developed, but their distribution is certainly interesting. In the Himalayas there are only two species with leptomorph rhizomes, *Arundinaria racemosa* Munro and *Chimonobambusa callosa* (Munro) Nakai. These species are restricted to the eastern end of the mountain chain, where rainfall is highest. The endemic species with long-necked pachymorph rhizomes, such as *Yushania maling* (Gamble) R.B. Majumdar, extend further west to areas where the rainfall is only moderate. They are also found at the western end of the Himalayas, where although the rainfall is lower, it is more evenly distributed, with more winter rain. In the central Himalayas, where spring rainfall is lowest, there are only unicaespitose bamboos.

This variation in distribution could be related to the ability of long rhizomes to penetrate through very dry soil during a spring drought. To reach up to several metres underground as well as producing tall culms, spreading bamboo rhizomes require a longer period during which growth is possible. Thus, the unicaespitose habit as seen in most Himalayan genera such as *Bambusa* Schreb. and *Drepanostachyum* Keng f. could be an adaptation to the driest conditions under which bamboos can grow. The pluricaespitose habit in pachymorph bamboos, as exemplified by *Yushania*, could reflect a combination of the ability to consolidate in one location when spreading is not possible, with the ability to spread when conditions are more suitable. The pluricaespitose habit in leptomorph bamboos, as seen in *Chimonobambusa* Makino and *Arundinaria* Michx., leads to an emphasis on spreading rather than consolidation, but is possible only when spring rainfall is more reliable. The true diffuse monopodial habit, as exemplified by the leptomorph rhizomes of many species of *Phyllostachys* Sieb. & Zucc. in their natural environments, is not indigenous to the monsoonal Himalayas, and may only occur where conditions are most favourable, in areas with ample rainfall more evenly distributed throughout the year, allowing sustained growth through spring, summer, and autumn.

The advantages of spreading bamboos over non-spreading types in suitable locations are apparent. Quick colonization of new sites is possible, and the sharp rhizomes can also penetrate the rooting systems of existing vegetation, with vigorous shoots benefiting from photosynthesis occurring elsewhere while they grow up to overshadow the vegetation at a different site. Such an effective vegetative dispersal mechanism may have implications for aspects of reproductive biology, for example length of flowering cycles, and the ability to survive flowering. Longer flowering cycles might be expected in spreading bamboos, with a reduced tendency for the plant to exhaust all reserves and die after producing too much seed. In addition, spacing of the culms may reduce parental competition and the benefits to seedlings of parental death, further encouraging polycarpy.

In the unicaespitose bamboos with pachymorph rhizomes dispersal is more reliant upon successful seed production. Short rhizomes cannot transport the plant very far. Dispersal can sometimes be effected above the ground by the rooting of branch bases when older culms fall down or arch across a stream. This may be one reason why the unicaespitose bamboos have retained relatively primitive, heavy branch architectures, while spreading genera such as *Phyllostachys* have developed more sophisticated and more efficient arrangements of their branches and foliage. The thickening of the pachymorph rhizome definitely allows greater storage potential, however, especially in those tropical bamboos that lose most of their leaves in an annual drought, and in these bamboos this is certainly a more important function of the rhizome than dispersal. Overall, as a broad generalization, pachymorph rhizomes clearly

represent a better adaptation to relatively dry conditions, with hard soils and periodic droughts.

The preponderance of primitive, iterauctant 6-stamened inflorescences in bamboos with pachymorph rhizomes has been taken to suggest that other characteristics of such bamboos are closer to the most primitive ancestors of today's bamboos, and therefore it has been conventional to treat pachymorph rhizomes as more primitive and ancestral, consequently considering leptomorph rhizomes to be relatively derived. Selection pressures upon the inflorescence and the rhizome are rather different, however, and there are pachymorph-rhizomed bamboos with 3-stamened semelauctant inflorescences, as well as leptomorph-rhizomed bamboos with 6 stamens or iterauctant inflorescences. It seems likely that all different rhizome forms would have evolved from ancestors with much less differentiation between culms and rhizomes, possibly with a more irregular scrambling or stoloniferous growth habit, rooting from most nodes. This might be closer to a leptomorph rather than a pachymorph rhizome system. It is very difficult to draw any conclusions as to which of these two rhizome forms would be more primitive. Today's leptomorph and pachymorph rhizomes may both be sophisticated modifications of ancestral rhizome forms. Moreover, bamboos with pachymorph rhizomes may have evolved independently from those with leptomorph rhizomes and/or vice-versa at different times in different subtribes, and there seems no reason why such developments would not be reversible. Comprehensive morphological and molecular phylogenetic analyses are required before any firm conclusions could be drawn.

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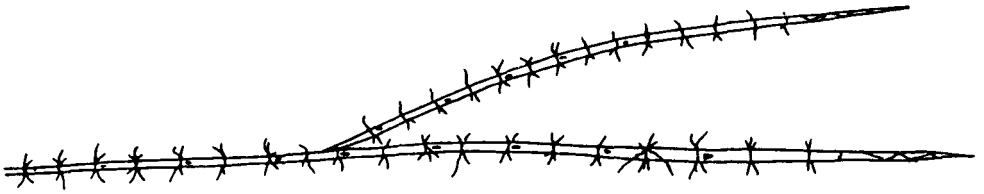
Figure 1. Rhizome branching pattern known as monopodial. The rhizome is leptomorph, with monopodial branching, and indeterminate growth. The culms may be diffuse or pluricaespitose, according to the degree of tillering at the culm base.
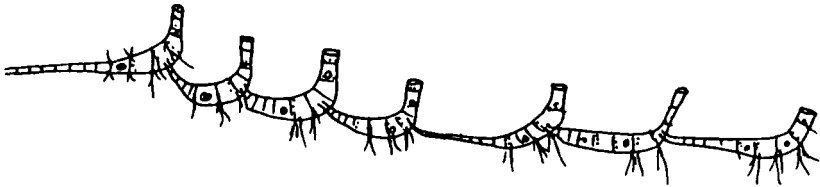
Figure 2. Rhizome branching pattern known as sympodial. The rhizome is pachymorph, with sympodial branching, and determinate growth. The culms may be unicaespitose, pluricaespitose, or diffuse according to the neck length and variability.
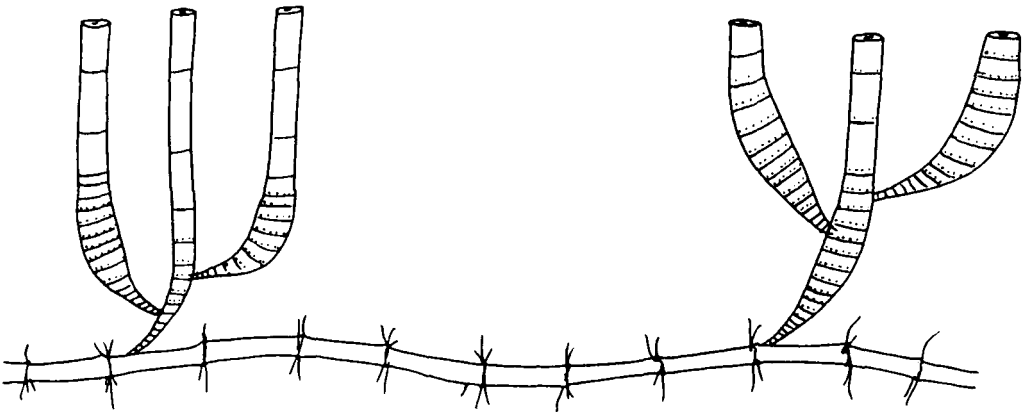
Figure 3. Rhizome leptomorph with monopodial branching and indeterminate growth, with tillering culms giving a pluricaespitose habit. This is often known as an amphipodial rhizome.
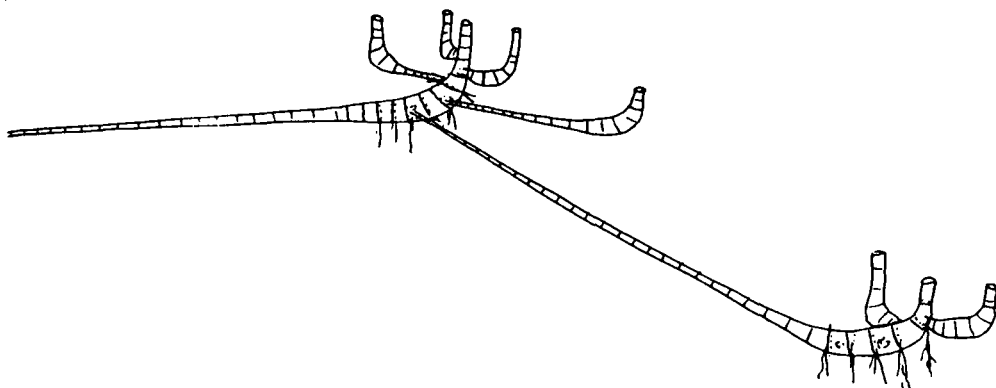
Figure 4. Pachymorph rhizome of *Yushania* with variable neck length, giving a pluricaespitose culm arrangement.
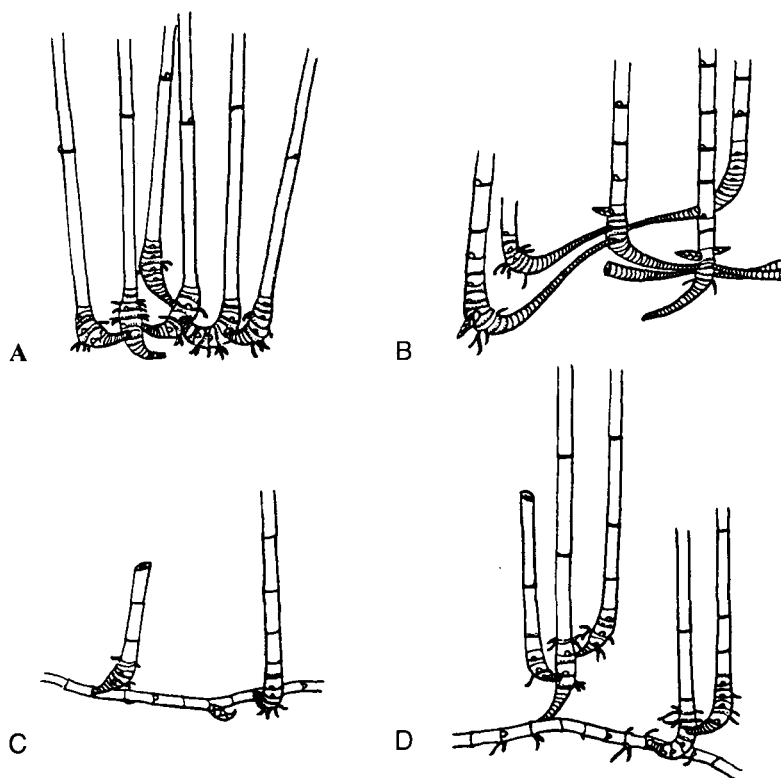
Fig. 5. Suggested terminology for four classic forms of rhizome and culm development. (Illustration from But et al., 1985, with permission of artist Mr. Deng Ying-feng)

    A – Rhizome pachymorph with short necks, culms unicaespitose.
    B – Rhizome pachymorph with consistently long necks, culms diffuse.
    C – Rhizome leptomorph, culms diffuse.
    D – Rhizome leptomorph, culms pluricaespitose.

T. Sekar, A. Balasubramanian, and V. Manimekalai[*]: **Vegetative propagation of an ornamental bamboo, *Bambusa vulgaris* cv. wamin McClure, by branch cuttings**

Abstract

Branch cuttings of an ornamental bamboo, *Bambusa vulgaris* cv. wamin, on treatment with PGRs at higher concentrations (1000-4000 ppm) resulted in shoot growth as well as root development. The present investigation reveals that the branch cuttings could be exploited for propagation without destroying the mother culms or rhizomes.

Introduction

Bamboos are ecologically, economically and socially important plants, with a wide spectrum of industrial and domestic applications, the most important being their use in the paper industry. Because of their long vegetative phases, monocarpic flowering behaviour and unpredictable seeding ranging from 3 to 120 years (Sharma, 1980) with a short viability period, they are more conveniently propagated by vegetative means and tissue culture techniques. However, for raising nursery stocks, cuttings and clumps have also been tried with varying success (Kamondo and Haq, 1988).

Vegetative propagation is commonly done by offsets and culm cuttings. Use of offsets has several limitations. The number of offsets available from a clump is very small and during its extraction damage may be caused to roots and rhizomes of the mother clumps. Propagation from 2 - to 3-year-old culms has been considered ideal (Seethalakshmi and Surendran, 1990). In the modern method of propagation through tissue culture, techniques have been standardized to get plantlets employing vegetative tissues as explants (Banik, 1983).

The above propagation methods have their own limitations. In propagation by cuttings from mature culms, mother culms are destroyed and the time duration for that establishment of roots and shoots is considerably long. Compared to vegetative propagation, the tissue culture technique is not economical and cannot be practiced with ease. Hence, the present work was attempted using juvenile cuttings without destroying the mother culms.

Materials and Methods

Bambusa vulgaris cv. wamin McClure (a cultivated ornamental bamboo) was chosen as the test plant. Cuttings from secondary and tertiary branches, 0.5 - 1 cm thick bearing three nodes were treated in the following plant growth regulators (PGRs): Indoleacetic acid (IAA), Indolebutyric acid (IA) and Benzylaminopurine (BAP), each with a concentration of 3000 and 4000 ppm. Naphthalene acetic acid (NAA) was used at 1000 ppm concentration. Cuttings were dipped in PGRs for 2 hours and planted vertically in polybags containing river sand. Control samples were soaked in distilled water before planting. The treated and control samples each consisting of ten replicates were kept in a humid chamber having a temperature of 37° C and 72% humidity. Cuttings were watered twice a day using a sprinkler. Bud release and the rooting behaviour were observed periodically.

The data on the shoot growth and root development were statistically analyzed using Analysis of Variance (ANOVA). Least Significant Difference (LSD) was calculated as suggested by Snedecor and Cochran (1967) (Table 1).

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Results and Discussion

Experimental results show that IAA and IBA bring about bud release and root induction in treatments with concentrations of 3000 and 4000 ppm respectively. Treatment with NAA at 1000 ppm results in pronounced development of roots with a delay in bud release. Cuttings treated with BAP showed profuse bud growth but without any root development. With regard to the number of roots and root length, NAA is found to be effective. Statisical analysis, Analysis of Variance (ANOVA), show that bud release, number of roots, and root length is significantly different between the various treatments. On the evaluation of bamboo regeneration techniques Kamondo and Haq (1968) reported that the performance of cuttings in the nursery was very poor. Use of rhizomes and clumps was more suitable and effective for raising bamboo.

So far experiments have been tried using PGRs with lower concentrations (not exceeding 100 ppm) using mother culms and side branches (Seethalakshmi and Surendran, 1990). It was shown that the side branch cuttings were slow in forming roots (Delgado, 1949). On the use of branch cuttings as planting material, Hasan (1977) has observed a limited success as compared to offsets. In the present investigation it is shown that the side branches could be successfully used as propagation material using higher concentrations of PGRs. Since profuse rooting is induced by NAA (1000 ppm) and more shoots develop in treatments with BAP (3000-4000 ppm) a combination of these two PGRs could be exploited for a better propagation protocol. Figures A-G show the response of juvenile stem cuttings to rooting and shoot development with different PGR treatments, after 60 days.

Acknowledgements

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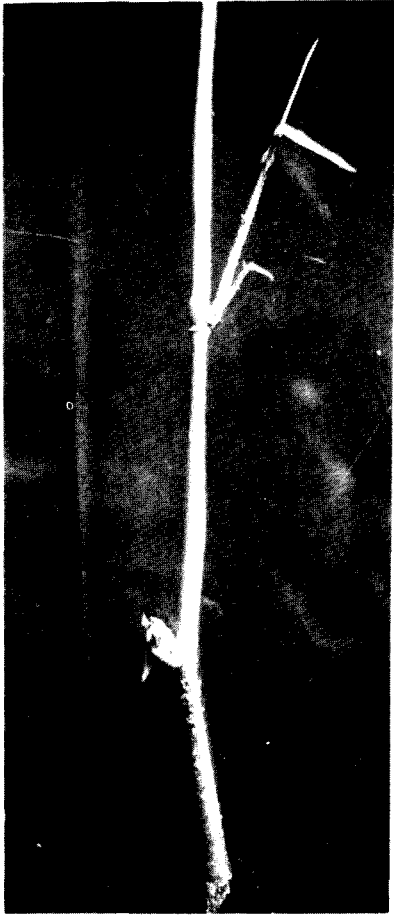

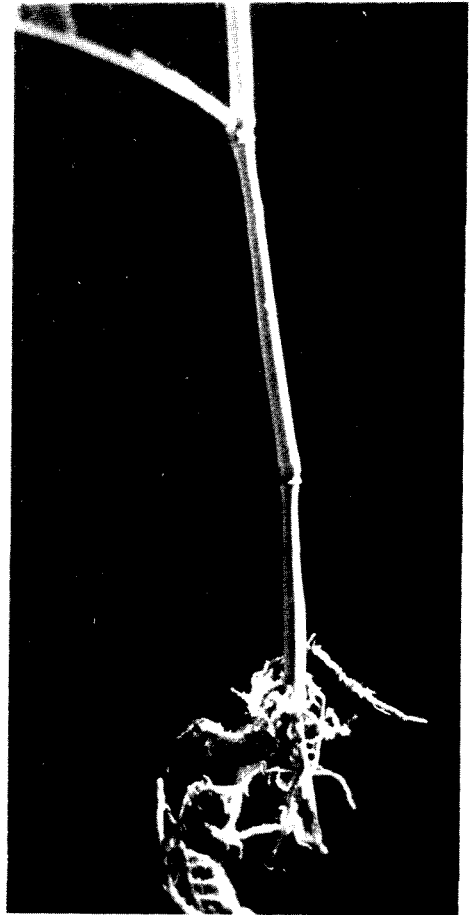Figure A. Control sample showing only shoot development.
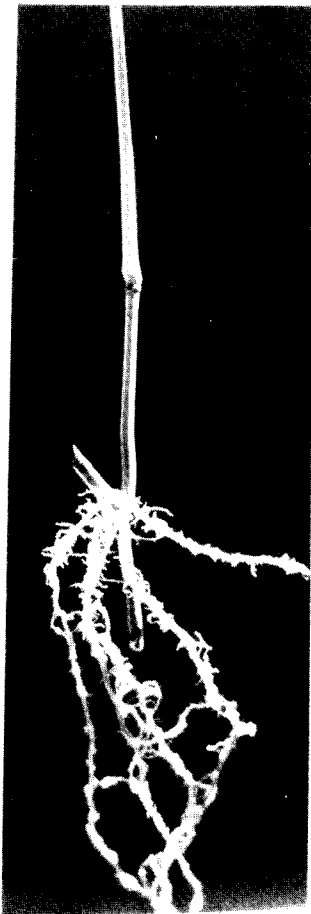
Figure B. IAA (3000 ppm) Showing rooting.

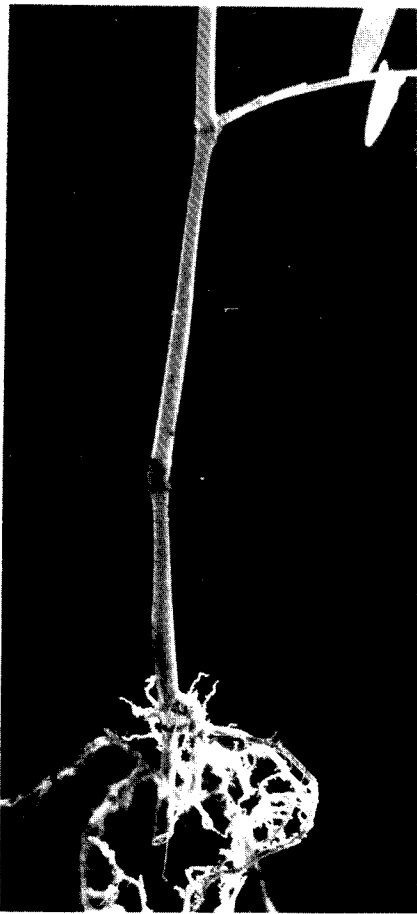Figure C. IAA (4000 ppm) showing increased root length.

Figure D. IBA (3000 ppm) showing rooting and shoot development.

Figure E. IPA (4000 ppm) showing rooting and shoot development.

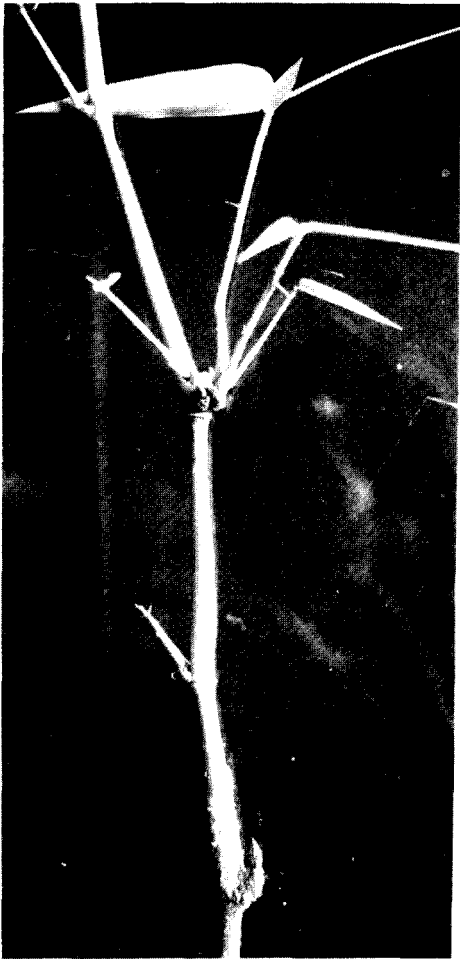Figure F. NAA (1000 ppm) showing profuse rooting.

Figure G. BPA (3000 ppm) showing
shoot development on all three nodes.

Table 1. Effect of plant growth regulators on bud release and root induction in cuttings of *Bambusa vulgaris* cv. wamin McClure (n - sample number   Xm - Mean   S.E. - Standard Error).

Treatments		Parameters					
		% Bud Release (n)	% Rooting (n)	Bud Release no. of days Xm±S.E. (n)	Rooting no. of days Xm±S.E. (n)	No. of roots/cutting Xm±S.E. (n)	Root length Xm±S.E. (n)
Control		30.00 (10)	-	28.33±0.43 (3)	-	-	-
IAA	3000 ppm	60.00 (10)	33.30 (6)	24.50±0.95 (6)	30.50±0.59 (2)	4.50±0.59 (2)	8.97±0.55 (9)
	4000 ppm	70.00 (10)	28.57 (7)	12.57±0.80 (7)	22.50±0.59 (2)	8.50±1.02 (2)	11.37±0.45 (17)
IBA	3000 ppm	60.00 (10)	33.30 (6)	24.00±0.06 (6)	29.50±0.59 (2)	3.50±0.59 (2)	10.90±0.65 (7)
	4000 ppm	80.00 (10)	62.50 (8)	15.00±0.82 (8)	24.00±0.6 (5)	11.80±0.50 (5)	11.80±0.36 (24)
NAA	1000 ppm	28.50 (10)	70.00 (10)	38.80±0.59 (2)	24.20±0.95 (7)	18.00±0.57 (7)	16.80±0.16 (126)
BAP	3000 ppm	70.00 (10)	-	21.70±1.98 (7)	-	-	-
	4000 ppm	70.00 (10)	-	21.40±2.28 (7)	-	-	-
ANOVA		-	-	F: 10.80 P<0.01 LSD: 9.53	F: 0.34 P>0.05	F: 25.07 P<0.01 LSD: 5.38	F: 35.42 P<0.01 LSD: 1.42

Ximena Londoño[*]: **A Decade of Observations of a *Guadua angustifolia* Plantation in Colombia**

Introduction

The objective of this paper is to provide background knowledge on the growth and development of a *Guadua angustifolia* Kunth crop. A 10-year follow-up study of *Guadua angustifolia*, from the beginning of its growth, was carried out in a coffee production region of Colombia. The study area is 155 kilometers north of Cali (Valle del Cauca), at an altitude of 1200 meters above sea level, in the Andean central Cordillera. Some aspects of its botany, ecology and uses are also presented.

Guadua is economically the most important bamboo in tropical America and has been associated with the New World agriculture since prehispanic times, approximately 5000 years B.P. Its historical importance can be traced back to archaeological remains of this plant found in human settlements associated with local cultures such as the Calima and Quimbayas (Salgado, 1986). Currently, it is known by popular names such as "guadua" in Colombia, "caña guadúa" in Ecuador, "yaripa" in Venezuela, "caña de Guayaquil" or "paca" in Peru, and "taboca" or "tacuara" in Argentina and Brazil.

According to the mythology of the Pantagoro tribe, located in the Department of Caldas in central Colombia, after the biblical universal deluge, only a single man was left to whom the "Am from Heaven" gave a guadua, which was suddenly transformed into a woman and companion (Patiño, 1977).

The first historical references to "guadua" were made by Christopher Columbus in September 1502, and the Spanish chroniclers Gonzalo Fernández de Oviedo, Bartolomé de las Casas, Juan de Castellanos and Jerónimo de Escobar in the 16th century. These authors mentioned the uses of and the extensive "bambú" forests between Panamá and the region of Guayaquil in Ecuador.

When crossing the Quindio region (Central Cordillera) in the famous expedition to visit the equatorial regions of Colombia, Alexander von Humboldt and Aimée Bonpland, travelling from Bogotá to Popayan in September-October 1801, noted extensive forest formations of guadua which dominated the landscape and vegetation of the lower lands. Impressed by this American plant, Humboldt wrote in his fieldnotes: "The bamboo and fern-tree are, of all the vegetable forms between the tropics, those which make the most powerful impression on the imagination of the traveler" (Humboldt, 1900).

In some Colombian regions, *G. angustifolia* has been closely related to local economic development. Early colonizers used this plant to satisfy almost all their needs in housing and domestic supplies. Several cities and towns such as Manizales, Pereira and Armenia were built with this plant. More recently, a new generation of architects, who are going beyond traditional architectural designs, have given great importance to this plant as a construction material by successfully experimenting with new joint systems and structural forms such as the arch, vault, and the arcade, among others.

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Taxonomy

Guadua is the largest bamboo in the New World. It belongs to the grass (Poaceae) family, more specifically to subfamily Bambusoideae, the Bambuseae tribe, Guaduinae subtribe, and *Guadua* genus. The Guaduinae subtribe includes the genera *Apoclada, Criciuma, Eremocaulon, Olmeca, Otatea,* and *Guadua.* The first three genera occur only in Brazil; *Olmeca* and *Otatea* in Mexico; and *Guadua* from Mexico to Argentina.

Guadua comprises the largest and most important bamboos in tropical America. It is endemic to America with approximately 25 species distributed from Mexico (22° 55'N) to northern Argentina (30°S), and it can be found at altitudes ranging from sea level to 2200 meters.

Guadua was first described by Kunth in 1822 as a segregate of the Asiatic genus *Bambusa.* Later, Munro (1868) listed some of its morphological features, and pointed out that the distinct geographical distribution could be used to differentiate *Guadua* from *Bambusa.* McClure (1973) recognized *Guadua* as a subgenus of *Bambusa.* However, after extensive morphological and anatomical studies carried out by Soderstrom and Ellis (1986), and Soderstrom and Londoño (1987), a number of characters have been clarified, thus allowing a better circumscription of this genus created by Kunth. Recently, according to L. Clark (1995), DNA sequences show *Guadua* as a separate genus, closer to other woody genera from the New World than to the Asiatic genera. Since the publication in 1868 of Munro's monograph which included only 13 species, *Guadua* has not been the subject of any detailed study. At present, approximately 21 species are recognized in the genus, some of them described in the last four years: *G. ciliata* Londoño & Davidse (1991), *G. calderoniana* Londoño & Judziewicz (1991), *G. chacoensis* (Rojas) Londoño & Peterson (1992), *G. sarcocarpa* Londoño & Peterson (1991), and *G. velutina* Londoño & Clark (1991).

The morphological and anatomical characters that make *Guadua* different from the rest of the bamboos are: 1) a triangular culm leaf in which the margins of the sheath and blade are contiguous or almost so; 2) a distinctive band of short white hairs both above and below the nodal line; 3) presence of stomata on the adaxial and abaxial surfaces of the leaf blade; 4) presence of papillae associated with the stomata on the adaxial surface of the leaf blade; 5) a palea of firm texture with prominent wings emanating from the keels; and 6) silica bodies saddle-shaped, narrow and elongated. Although the presence of thorns is ubiquitous, it cannot be considered a generic character but a specific one (Londoño, 1992).

It is possible to distinguish two groups within *Guadua* based on their growth habit: 1) those with erect culms and, 2) climbing and hanging culms.

Species with erect culms are characterized by a) erect habit, or slightly bent over; b) well-developed sympodial rhizomes; c) stout woody culms, usually hollow with thick or thin walls, between 7 and 30 meters in height and 5 to 20 centimeters in diameter, and d) a single branch angled (45° to 50°) upward. Most species of *Guadua* belong to this group. These are, *Guadua angustifolia* from the Andean regions of Colombia, Ecuador and Venezuela; *G. aculeata* from Central America; *G. velutina* from eastern Mexico with the most northern distribution within the genus (22° 55'N and 99° 12'W); *G. amplexifolia* from Central America, northern Colombia and Venezuela; *G. paniculata* (with the widest distribution) ranging from Mexico to Bolivia; *G. latifolia* from the Río Negro in Venezuela; *G. superba* from the Amazonian forests of Colombia, Brazil and Peru; *G. weberbaueri* from the tropical rainforest of Brazil, Colombia, Peru and Venezuela; *G. sarcocarpa* from the Amazonian forest of Brazil and Peru (distinguished by its fleshy fruit, a unique character within the genus); *G. calderoniana* endemic to Bahía and Espírito Santo in Brazil; *G. tagoara*, abundant in Rio de Janeiro and São Paulo in Brazil; *G. trinii, G. paraguayana*, and *G. chacoensis* from southern Brazil, Bolivia, Paraguay and northern Argentina. *Guadua chacoensis* is the most austral species of this genus (30° S).

The species with climbing and hanging culms are characterized by their a) clambering habit; b) more weakly developed sympodial rhizome, these short or elongated; c) slender, woody culms either hollow or solid, from 3 to 12 meters in height and 1 to 5 centimeters in diameter; d) a single dominant branch per node, angled upward or adpressed but not more than 45°, extending over the surrounding vegetation up to approximately 7 meters. Three species belong to this group: *Guadua glomerata, G. ciliata,* and *G. maclurei.* The first two species are found along the river edges and creeks in Amazonia, in areas known as "varzea" or "igapó". The third one, *G. maclurei,* is found only in Central America.

Ecological Distribution

Guadua has one of the widest geographical distributional ranges in America, second among the neotropical woody bamboos only to *Chusquea.* It extends from Mexico and all of the Central and South American countries to Argentina with the exception of Chile, up to 2200 meters above sea level. McClure (1973) states that *Guadua* reaches its peak under meso-phytic conditions at altitudes of 1500 meters. Temperature seems to be a limiting factor in the latitudinal and altitudinal distribution of this species due to its lack of adaptation to prolonged periods of temperatures below 0° Celsius. Most of these species occupy diverse habitats in the vegetation communities of the tropical rainforest, wetland and humid lowland forests, and humid premontane tropical forest. Other species such as *Guadua amplexifolia* and *G. paniculata* grow in gallery forest communities in dry tropical forest. Precipitation is another important climatic factor related to *Guadua*'s growth. Most of the species grow in areas with annual precipitations above 1200 mm. However, species like *Guadua paniculata, G. trinii* and *G. amplexifolia* grow in areas with annual precipitation between 500 and 600 mm. *Guadua* species prefer sandy-limey and clayish soils, and alluvial river banks. These can be generally observed along the river terraces and creeks, in well drained soils; however, some species such as *Guadua glomerata* and *G. ciliata* prefer swampy or humid areas.

Among all American bamboos, *Guadua angustifolia* is considered the most versatile and useful species, with a relatively high resistance to both fungi and wood-eating insects (McClure, 1953). The optimal environmental conditions for its growth and development are altitudes between 0-1500 meters, and temperatures between 20° and 26° Celsius; well distrib-uted year-round precipitation between 1300 and 4000 mm; a relative humidity of about 80%; and sandy and clayish soils, rich river edges being preferred. Daily temperatures below 11° Celsius for longer than 6 hours are a limiting factor (Londoño & Prieto, 1983).

Vegetation communities dominated by *G. angustifolia* are known as "guaduales." Mem-bers of the Piperaceae, Rubiaceae, Araceae, Mimosaceae and Compositae plant families are found in their interior where 57% of the associated species are located in the herbaceous stratum. In addition to preserving the soil and environmental humidity, this vegetation pro-vides organic matter and food to the associated fauna. Because they are located at an altitudi-nal range where native forest is being gradually destroyed, "guaduales" have become shelters for animals like anteaters, howler monkeys, squirrels, armadillos, woodpeckers, chachalacas (a guanlike bird), and a diversity of insects.

Due to their rhizome morphology (pachymorph) and to its expanding and growing root system at about 50 centimeters underground, "guaduales" play an important role in the pro-tection of hydrographic basins, contributing to reduced cliff erosion which maintains the river channel and flow, and protecting the established flora and fauna as well.

Management

Colombian research institutions and regional corporations committed to the conservation, propagation and rational management of *Guadua angustifolia* have developed a variety of conservation strategies to reduce the over-exploitation of vast "guaduales."

Thus, a silvicultural program has been established for the management of the existing native "guaduales" oriented to obtaining practical knowledge of this species such as optimal cutting method and intensity of cutting, availability cycles, and clearing area. It is estimated that there are 15,000 ha in the Colombian Andean Zone, of which 1500 ha are being exploited.

Sexual and asexual propagation including "in vitro" propagation have been experimented with in newly established *Guadua* plantations. These propagation types can be described as follows:

a) Sexual propagation: *Guadua* propagation from the seed. *Guadua angustifolia* seeds are dry caryopses. Although the flowering of *G. angustifolia* occurs every year after a dry period, seed gathering becomes difficult because a high percentage of spikelet florets tend to be parasitized at an immature stage by insect larvae of the Diptera and Hymenoptera orders. Seed propagation experiments have provided a high percentage of germination, between 95-100%. This method of sexual propagation is difficult to practice due to the difficulties of gathering the seeds.

b) Asexual propagation: Based on the propagation of *Guadua* by taking vegetative plant sections such as stems, branches, shoots and roots. Asexual reproduction is the most recommended and widely utilized system in *G. angustifolia* studies based on this method, which were carried out by Castaño (1987), Manzur et al. (1980), and by the Regional Corporations of Quindío, Caldas, Risaralda and Valle. Out of ten asexual experimental methods only three fulfilled the requirements of being efficient, fast and economical for large-scale reforestation initiatives. These are: a) thin stems with a portion of the basal rhizome cultivated on a substratum layer of composted soil or "cenichaza"; b) segments of thorny lateral branches from the lower culm portion; and c) in-vitro culture methods, which are developed in the laboratory under aseptic conditions by using apical and axillary meristems placed in an in-vitro medium that was hormonally enriched (Manzur, 1986).

The Study Area

This research is based on a 0.02 ha. (16 X 12 meters) experimental plot or "guadual" located at 4° 34' N and 75° 47' W, at La Esmeralda farmhouse, Municipality of Montenegro, Department of Quindío, Colombia. It is at 1250 meters above sea level, has an annual precipitation of 2042 mm, and relative humidity of 77%; and its topography is flat with typical dystrandepts soil with a high content of volcanic ash, a loose-sandy texture, and a pH of 5.45.

Twenty plants, each 30 centimeters in height, were placed in this 0.02 ha. plot. This was under the asexual propagation method; i.e., with a portion of its basal rhizome cultivated on a substratum layer of composted soil. Prior to and during this study, the following plowing practices were made in the *Guadua* plot: a) complete terrain clearing; b) layout and square pit location of plots on a 4 x 4 meter grid (i.e., 625 plants/ha). c) pits 30 cm x 30 cm, 30 cm in depth; d) complete underbrush clearing approximately every three months, the presence of weeds carefully avoided during the first two years; e) thorny lateral branches were cut at the end of the third year in order to facilitate data gathering. Application of fertilizers was completely avoided in this experimental assay.

By the end of the first two years of cultivation (1981-1983), the average diameter of culms in the *Guadua* plot was 0.5-1 cm, with the average height 1-1.5 m. At year four (1985), the average diameter of culms in the plot was 7.45 centimeters, average height 5-10 meters,

and density 10,938 culm/ha. After seven years of cultivation (1988), the average diameter of culms in the *Guadua* plot was 8.44 centimeters, average height 10-15 meters and a density of 14,406 culms/ha. In 1991, ten years after this experimental *Guadua* plot was open, the average diameter was 9.45 centimeters, average height 15-18 meters and density 19,031 culms/ha (Table 1, Fig. 1).

A character of *Guadua*, a monocotyledonous plant, is the lack of vascular cambium. As such, it emerges with a defined diameter whose growth is expressed only in height and wood maturity. Four developmental phases have been established for *Guadua angustifolia* (Castaño, 1987): 1) new shoot phase, 2)juvenile phase, 3) mature phase, and 4) overmature or dry phase.

1. New shoot phase: it starts with the emergence of the new shoot until it reaches its maximum height. It is always protected by the culm leaves, without developing branches or foliage. This phase lasts 6-7 months. The growth follow-up of new shoots, between July 1986 and July 1987, produced the following average results: a) a growth rate of 30-40 centimeters during the first 0-15 days, equivalent to 2.7 cm/day; b) a height of 1.82 meters was reached during the following 16-88 days, equivalent to an increase of 3.1 cm/day and 0.91 meter/ month; c) between 89-147 days (2.5-4.5 month), a height of 5.35 meters was reached, which is equivalent to an increase of 8.6 cm/day or 2.7 meters/month; d) at 137-164 days (5th-6th month), the new shoot reached a height of 11 meters, with an increase of 11cm/day and 3.3 meters/month; e) between days 164-198 (6th-7th month), the new shoot height reached 14.1 meters, with an increase of 9 cm/day and 2.7 meters/month. Once the new shoot reaches its definite height, it starts the juvenile phase (Fig. 2).

2. Juvenile phase: it can be identified by the loss of the culm leaves, the culm's intense green color, and by the development of branches and foliage. This is a three-month long phase. The lateral branches in the upper portion begin to emerge at 210-230 days, and the foliage formation begins to completely develop at 230-250 days, i.e., 7th and 8th month.

3. Mature phase: the culm loses its bright green color, turning into an opaque green and then gradually turns gray as lichens, fungi and mosses appear over the culm. The identification of this phase is subjective since parameters different from ascomycetes and bryophytes for precise culm dating haven't been found. The time period for this phase is from 1.5 years when grey stains of rounded lichens appear over the culm, up to year five when large quantities of lichens colonize the internodes, and the presence of mosses, fungi and gray, pink, and blue lichens begin to spread. This mature phase is appropriate for *Guadua* harvesting.

4. Overmature or dry phase: this is the plant death phase. It is expressed in the yellow color of the culm, and dryness of the middle portion of the branch. The time period for this phase is from 5 to 7 years.

Conclusion

The native guadual employed as a control in this study for comparative purposes is located in the same region. It shows an average diameter of 12.5 centimeters and density of 6594 culms/ha (Table 1). This guadual of unknown age has not been subject to any kind of technical management. Comparatively, the cultivated *Guadua* in the experimental plot exhibits a density three times higher within a 10-year period. A possible explanation for this observation is that plant distance and time are critical factors for cultivated *Guadua* growth and development. From this, it can be hypothesized that longer periods and technical management (e.g., plant cutting, cycle and intensity of cutting, etc.) define density of *Guadua* plantation. It can be expected that native guaduals show a tendency to decrease the production and diameter

of new shoots; therefore, soil saturation due to competing factors is produced. It is suggested that the cultivation distance of *Guadua angustifolia* for commercial purposes should be from 6 to 10 meters between lines and 4 to 6 meters between plants within a line so that greater sunray incidence can reach the plant. On the other hand, for conservational purposes the cultivation distance between lines and plants should be shorter and in accordance with degree of slope. It is expected that in a large-scale management program for *Guadua*, a vast number of new shoots might occur, higher quantities of juvenile culms, and the absence of dry culms.

Guadua is an alternative cover crop in Colombia, mainly along river edges, streams and creeks for erosion control. Unfortunately, in spite of its well understood role, the lack of local incentives from decision-making institutions to cultivate this valuable natural resource is making a critical negative impact. Its role is crucial in construction and housing programs, in agriculture, as supplies for domestic handicrafts, and most importantly, in environmental conservation.

Acknowledgements

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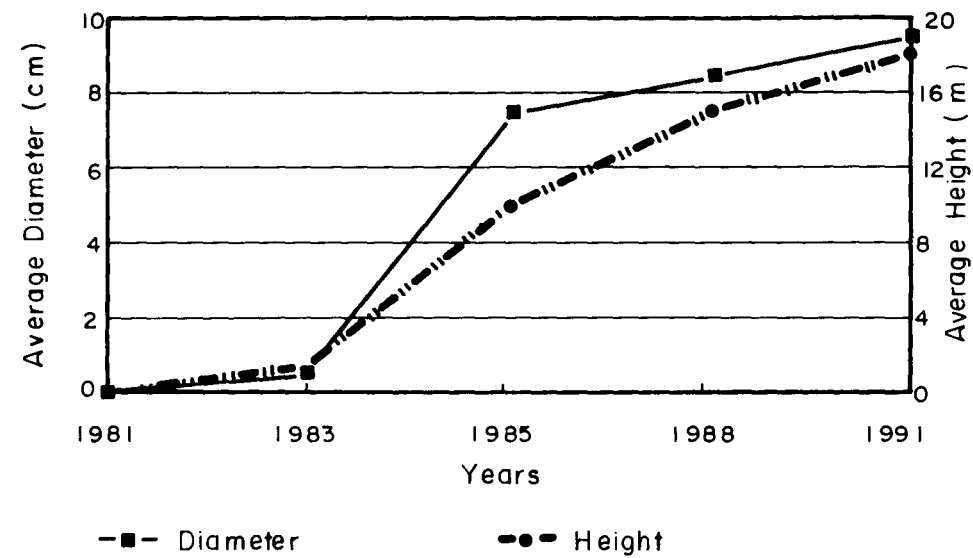
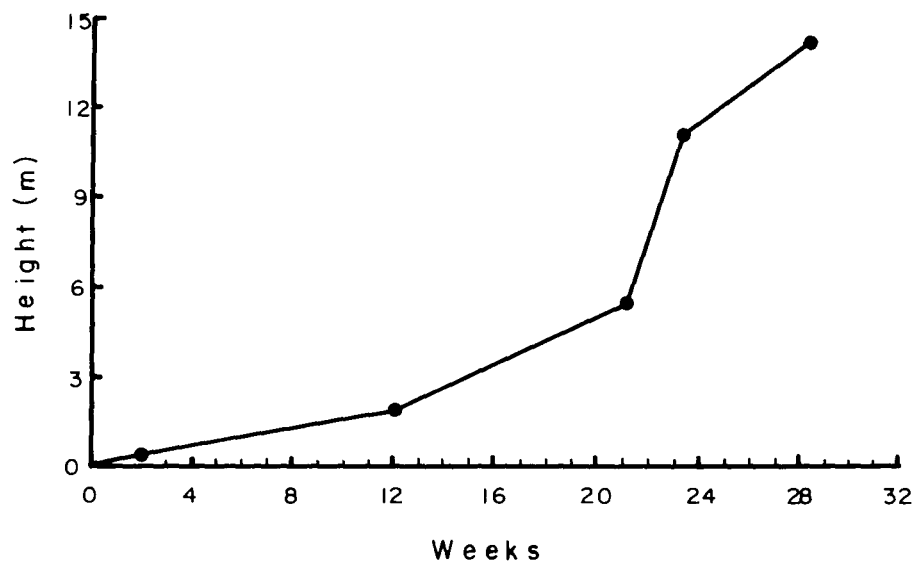Figure 1. Growth development; *Guadua angustifolia* crop.

Figure 2. New shoot development phases; *Guadua angustifolia* crop.

Table 1. Growth Phases

Time	NS		J		M		OM		Total		Density
Period	φ	%	φ	%	φ	%	φ	%	φ	n	c/ha
*4 years	7.7	16.0	8.4	13.1	6.8	70.9	0	0	7.6	350	10,938
*7 years	9.3	11.1	9.7	16.9	7.7	71.4	7.8	0.6	8.6	461	14,406
*10 years	9.6	7.2	10.1	16.3	9.6	73.1	8.3	3.4	9.4	609	19,031
NG 1981	13.7	9.1	13.0	9.1	12.8	74.8	9.0	7.0	12.5	211	6,594

Key: NS = New stock   NG = Native guadual
      J   = Juvenile   c/h = Culms/hectare
      M   = Mature   φ   = Average diameter
      OM = Over mature   n   = Culms/clump
      *   = Cutivated guadual

Comparative data between cultivated and native guadual in Colombia. Culm percentages and average diameter in growth developing phases.

T. Sekar and A. Balasubramanian*: **Diversity of Culm Bundles in**
***Bambusa vulgaris* Schrader ex Wendland**

Abstract

Bamboos are an unique group of perennial, giant, arborescent grasses belonging to the family Poaceae, which grow mostly in tropical, subtropical and temperate regions of the world. Being a versatile multipurpose forest product, bamboos have occupied a place of pride in the vegetation of the country, playing a vital role in the world's industrial and domestic economy [Varmah and Bahadur, 1980]. To the taxonomist, bamboo poses special problems in identification since taxonomic differences in plants are primarily based on reproductive structures. Bamboos, however, usually flower only once, namely at the end of their life span of about 20-40 years. Because of the rarity of flowering and the suppression of vegetative activity during flowering, emphasis has been made on the need for the usage of vegetative parts for identification and classification [Holtum, 1958; McClure, 1966; Grosser and Liese, 1971].

Introduction

Anatomical characteristics of the culm have been employed as useful guides in bamboo taxonomy. Variations in the features of culm epidermis, fibrovascular bundles and the inner lining cavity are employed in classification of bamboo (Li et al., 1962; Pattanath and Ramesh Rao, 1969; Gosh and Negi, 1960, and Chauhan et al., 1988, 1989). Liese (1987) in reviewing the anatomy of the bamboo culm described four types of vascular bundle organization based on the nature and the extent of association of sclerenchymatous tissue with the vascular strand.

Type I - Central vascular strand plus supporting tissue sclerenchyma sheath.

Type II - Central vascular strand plus supporting sheath, protoxylem sheaths strikingly larger.

Type III - Central vascular strand plus supporting sheath plus separate protoxylem cap.

Type IV - Central vascular strand plus supporting sheaths plus separate phloem and protoxylem caps.

A new type of fibrovascular bundle (Type IIA) which is composed of the central vascular strand and a strikingly larger phloem sheath has been reported in *Bambusa vulgaris* cv. wamin (Sekar and Balasubramanian, 1993). The variation of bundle organization across the culm wall was used in the classification of bamboos by Grosser and Liese (1971, 1973) and Zamuco (1973). Pattanath and Ramesh Rao (1969) in their study on the culm anatomy have taken into account the homogeneous or heterogeneous nature of the cortex and the nature of the inner lining cavity besides bundle types in the delimitation of Indian bamboos.

Fibre characteristics of culms which were reported in several species of bamboo by Medina and Ciaramello (1962), Liese and Mende (1969), Liese and Grosser (1972), Pattanath (1972), Espiloy (1982), Abd. Latif et al. (1960), and Abd. Latif and Mustafa (1992) is yet another criterion used in bamboo taxonomy. Septation in fibres recorded in *Dendrocalamus* and *Cephalostachyum* was found to be a valuable character for identification (Parameswaran and Liese, 1977).

In the present investigation the structural variations and the fibre characteristics in mature culm internodes of the infraspecific taxa of *Bambusa vulgaris* have been compared and

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their delimitation attempted in order to evaluate the taxonomic position of the varieties.

Materials and Methods

Mature culm samples of the taxa investigated (viz. *B. vulgaris* Schrader ex Wendland, *B. vulgaris* var. *striata* (Lodd. ex Lindl.) Gamble, *B. vulgaris* cv. wamin McClure) were collected from the germ plasm maintained at Forest Research Institute (FRI), Dehradun and Kerala Forest Research Institute (KFRI), Peechi. Six samples from each member were collected uniformly from the 5th mid-internode of 3-year-old culms as per the standard procedures of collection (McClure, 1989). Conventional methods of sledge microtomy maceration and staining were followed (Johansen, 1940; O'Brien and McCully, 1981). The data on the morphology and distribution of fibro vascular bundles and the fibre characteristics were compared.

Results

In general the mid-internode of the culm in bamboos shows an outermost layer of compactly arranged epidermis followed by a narrow or wide homogeneous (or) heterogeneous cortex enclosing a wide fibrovascular bundle region with a distinct or indistinct inner lining zone composed of parenchyma or sclereids.

The members of *B. vulgaris* investigated uniformly show a compactly arranged thick-walled epidermis. The organization of the cortex shows variation among the taxa. A wide cortex composed of parenchymatous cells enclosing fibre strands and a concentric type of fibrovascular bundles is characteristic of *B. vulgaris* cv. wamin. The cortex is homogeneous in *B. vulgaris* and heterogeneous in *B. vulgaris* var. *striata* and *B. vulgaris* cv. wamin.

The fibrovascular bundle region, which could normally be separated into outer, middle and inner regions is varied in the organization and distribution of vascular bundles. At the outer region bundles are smaller, completely ensheathed by fibrous tissue and with higher frequency of distribution. In *B. vulgaris* var. *striata* and *B. vulgaris* cv. wamin, the outer region shows prominent fibre strands alternating with fibrovascular bundles. The fibre strands are absent in *B. vulgaris*. In the middle region, bundles are much larger with a low frequency and represent the typical bundle type. *B. vulgaris* shows the bundle type IV and *B. vulgaris* var. *striata* the type III. In *B. vulgaris* cv. wamin bundle type is IIA in which the phloem sheaths is strikingly prominent (Figure 1 and Table 1). At the inner region of the culm wall, persistence of the protoxylem cap and disorientation of bundles are observed in *B. vulgaris* var. *striata* and an absence of protoxylem cap in *B. vulgaris*. In all the three members the inner lining cavity is distinct and composed of 5-6 tangential rows of thick-walled parenchyma cells. But *B. vulgaris* cv. wamin is distinct in having two zones of parenchyma.

Four types of culm fibres, viz. very thick, thick, thin, and very thin walled, are observed in *B. vulgaris* and *B. vulgaris* var. *striata*. Septate fibres occur only in *B. vulgaris* cv. wamin. The wall lamellation varies from 3-10 layers, the pitting being uni-biseriate in all the three taxa.

Discussion

The best utilization of bamboo depends on the appraisal of morphological, anatomical, physico-mechanical and chemical properties of the culm. The properties of bamboo are mainly determined by the structure of culm, but in spite of its wide use, knowledge of its anatomy is still rather limited. Little is known about the possibility of differentiating bamboo species on the basis of their anatomical characteristics or about the structural variability within one culm as well as between culms of one species (Grosser and Liese, 1971). Grosser and Liese (1973) state that significant anatomical differences exist between species of a genus and between genera. Grosser and Liese (1973), on the importance of culm anatomy in classification, have

remarked that "Because many bamboo species flower only rarely, classification systems based solely on reproductive characters, such as those of Munro (1868), Benthem (1883), Gamble (1896), E.G. Camus (1913), A. Camus (1935) and Holttum (1956) have limited value for the identification of standing culms ... Consequently, more emphasis should be placed on anatomical structure, because significant anatomical differences exist between species of a genus and between genera. These differences can be applied successfully for the designation of bamboo genera into natural systematic units and for the further development of a modern bamboo classification."

Variation in the cortex has been explored as a taxonomic character for distinguishing various species of *Bambusa, Dendrocalamus, Melocanna* and *Thyrostachys* by Pattanath and Ramesh Rao (1969). *Bambusa* species were shown to possess both homo- and heterogeneous cortex types. The present investigation revealed a heterogeneous cortex in *B. vulgaris* var. *striata, B. vulgaris* cv. wamin and was homogeneous in *B. vulgaris*. The presence of a wide parenchymatous cortical zone enclosing fibrovascular bundles and fibre strands distinguishes *B. vulgaris* cv. wamin from the other two members.

In hollow culms, a zone of non-vascular tissue lining the pith cavity may sometimes show striking differences which are useful in distinguishing taxa (Pattanath and Ramesh Rao, 1969). The present study on *Bambusa vulgaris* showed variation in the organization of lining cavity. Though it is parenchymatous in nature the lining cavity is made up of two zones in *B. vulgaris* cv. wamin, unlike the other two taxa.

In characterizing a bamboo species Grosser and Liese (1971) suggested that it is not only necessary to identify the existing vascular bundle types but also their vertical variation within the whole culm and proposed the vascular bundle diagram. Variation of bundle organization across the culm has also been taken into account and, based on the persistence or the disappearance of the protoxylem cap at the inner region of culm wall, six patterns have been derived for the several bamboos studied (Sekar and Balasubramanian, 1993). Bundle pattern along the axis of the culm from base to top is of restricted value, since variation does not exist along the axis. But the change in the organization between different regions of mature culm, from outer to inner, has revealed a meaningful pattern, which is consistent and characteristic of each taxon. In the outer region there is a common sclerenchymatous sheath which surrounds the vascular strands. Subsequently, the phloem sheath separates and the xylem elements are enclosed by a common sheath. The bundles at the middle region showed separation of protoxylem and metaxylem sheaths and the development of additional sclerenchyma strands (phloem and protoxylem caps) resulting in the typical organizational type. At the inner region the protoxylem cap may persist or disappear, characteristic of species. The types of bundles and the pattern are of diagnostic value at the species level, though not at the generic level. Further, the types could be varied within a species, *B. vulgaris* with type IV, *B. vulgaris* var. *striata* with type III and *B. vulgaris* cv. wamin with type IIA. The comparison of culm anatomy in the above taxa is shown in Table 1.

Fibres in culm internodes of most species occur as sheaths and caps in association with vascular strands besides being distributed as isolated strands in some species. In *B. vulgaris,* var. *striata,* fibre strands form paths alternating the fibrovascular bundles at the outer region of culm wall. In *B. vulgaris* and *B. vulgaris* cv. wamin, fibre strands are distributed in the cortical parenchyma. With regard to fibre types all the four types are observed in *B. vulgaris* and *B. vulgaris* var. *striata,* whereas in *B. vulgaris* cv. wamin thick and very thin-walled fibres are present. Among the three taxa septate fibres are observed only in *B. vulgaris* cv. wamin.

Systematic position of *Bambusa vulgaris* var. *striata,* and *B. vulgaris* cv. wamin.

Several authors including Gamble (1896), Camus (1913) and Holttum (1958) recognized *Bambusa vulgaris* var. *striata* as an infraspecific taxon and treated this as a variety. Based on morphological characters, Munro (1868) treated it as a species distinct from *B. vulgaris.* Rivière (1879) treated this as var. *vittata* and Blatter (1929) included this variety as a synonym of var. *striata.* Anatomical details shown below lend support in treating this taxon as a species instead of as a variety.

1. A narrow zone of cortical parenchyma.
2. Bundle type III with a separate protoxylem cap.
3. Persistence of protoxylem cap at the inner region.

Many botanists treated *Bambusa vulgaris* cv. wamin as a cultivated variety of *B. vulgaris.* Brandis (1899) described this under the Burmese name "wamin". Camus (1913) treated this as a species from *Bambusa vulgaris* in view of its distinctive morphological characters but with a question mark. McClure (1966) did not support the view of Brandis and Camus. Bennet and Gaur (1990) treated this as a separate species, *Bambusa wamin* and not a variety. The present study on culm anatomy upholds the view of Camus (1913) in treating "wamin" as a species based on the following features:

1. A wide zone of cortical parenchyma in which tracheary elements ensheathed by sclerenchyma and isolated fibre strands of different sizes are distributed.
2. Distinct type of bundle organization (Type II-A) in which the phloem sheath is strikingly prominent.
3. Metaxylem sheaths are composed of rectangular thick-walled parenchyma cells.
4. Presence of septation in fibres.

B. vulgaris is distinct from *B. striata* and *B. wamin* in (i) the presence of IVth type of vascular bundle, (ii) a homogeneous cortex, (iii) the absence of fibre strands at the outer region and (iv) the disappearance of protoxylem cap at the inner region.

Summary

Bambusa vulgaris is one of the valuable and much-used bamboos for structural purposes and in the paper industry. The variations in fibrovascular bundle organization, mechanical tissue distribution and the fibre characteristics in culm internodes have been used for the identification and delimitation of *Bambusa vulgaris* Schrader ex Wendland and its varieties (viz. *B. vulgaris* var. *striata* (Lodd. ex Lindl) Gamble and *B. vulgaris* cv. wamin McClure). The significance of the structural diversity of the culm wall in taxonomy is discussed and the elevation of the above varieties to the species level is supported.

Acknowledgements

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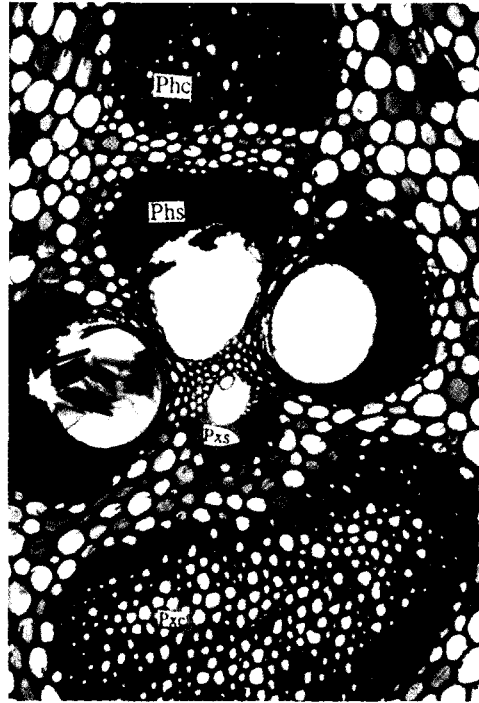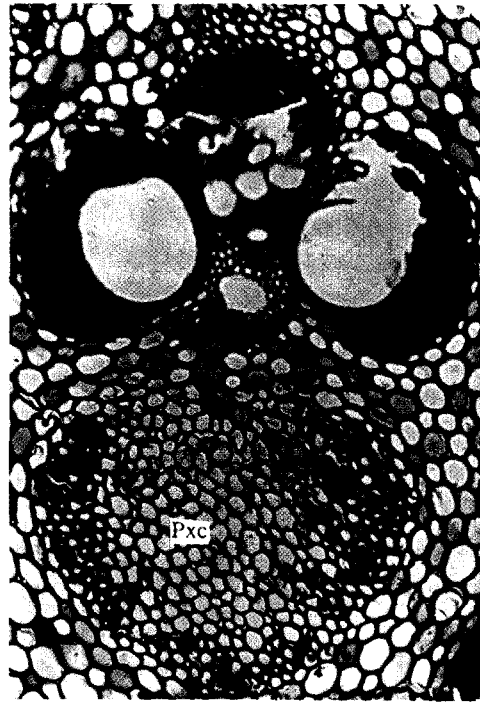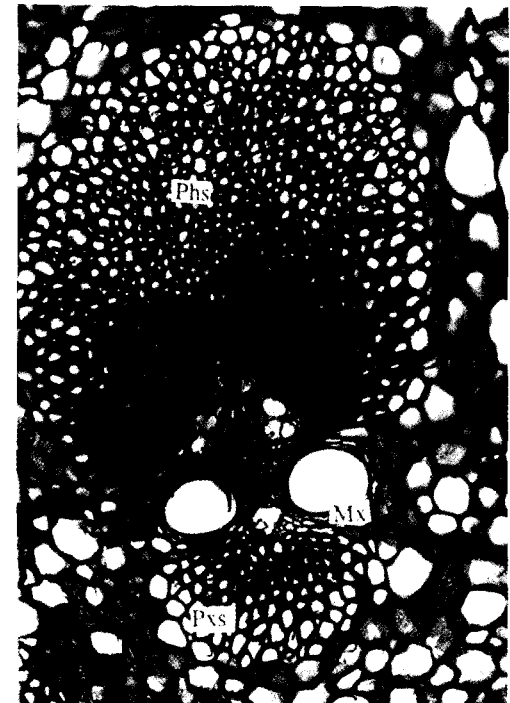
A   B   C

Figure 1. A-C Fibrovascular bundle organization in the culm internode x 200

A. Bundle Type IV in *B. vulgaris*

B. Type III in *B. vulgaris* var. *striata*

C. Type IIA in *B. vulgaris* cv. wamin

Ph - Phloem, Phs - Phloem sheath, Px - Protoxylem, Mx - Metaxylem, Phc - Phloem cap, Pxc - Protoxylem cap, Pxs -Protoxylem sheath.

Table 1. Comparison of the culm internodal structure.

Characters	*Bambusa vulgaris*	*Bambusa vulgaris* var. *striata*	*Bambusa vulgaris* cv. wamin
Cortex	Homogeneous and abscence of fibre strands	Heterogeneous with fibre strands	Heterogeneous wide zone of cortical parenchyma with concentric bundles and isolated fibre strands
Fibrovascular	Type IV	Type III	Type II A
Metaxylem sheath	Composed of sclerenchymatous tissue	Composed of sclerenchymatous tissue	Composed of rectangular thick walled parenchyma cells
Cap behaviour at the inner region	Disappearance or protoxylem cap	Persistence of protoxylem cap and disorientation of bundles	Cap not separate
Lining cavity	Homogeneous and single zone	Homogeneous and single zone	Homogeneous and two zones
Fibres	Non-septate	Non-septate	Septate
Taxonomic treatment	Schrader ex Wendland, 1810 *B. vulgaris*	Gamble, 1886 Camus, 1913　　　*B. vulgaris* Blatter, 1929　　　var. *striata* Holttum, 1958 Rivière, 1879　　　*B. vulgaris* var. *vittata* Munro, 1968　　　*B. vulgaris* Sekar &Balasubrmanian 1993　*B. vulgaris*	Brandis, 1905　　　*B. vulgaris* cv. wamin Bennet & Gaur, 1990　　*B. wamin* Sekar & Balasubramanian 1993　*B. wamin*

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Cover: *Guadua angustifolia*