ASPECTS OF BAMBOO AGRONOMY

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Various aspects of the growth and development of bamboo are reviewed, including growth cycles of plant parts, effects of aging on important plant tissues, uptake of water and nutrients, photosynthesis, storage and translocation of photosynthates and nutrients, and accumulation and partitioning of biomass and nutrients. Also discussed are how these aspects can be manipulated with agronomic techniques, such as management of standing-culm density, culm-age structure, leaf area, and leaf-age structure. Selected aspects of how the environment (i.e., water availability), soil physical properties (such as slope, texture, bulk density, moisture-holding capacity, and soil temperature), and soil chemical properties (such as pH, salinity, and nutrient availability) impact on bamboo production are outlined. This review also discusses how the environment can be managed with irrigation, terracing, tillage, covers and mulches, canopy adjustments, and fertilization with optimal amounts of nutrients, nutrient ratios, schedules, and forms of fertilizer.

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I. INTRODUCTION

Over 70 genera of bamboo with over 1200 species occur in natural forests, semi-exploited stands, and intensive plantations, covering an area of more than 14 million ha worldwide (Dransfield and Widjaja, 1995; Fu and Banik, 1995). Eighty percent of the species and area are confined to South and Southeast Asia and mostly in China, India, and Myanmar. China, with the largest bamboo industry worldwide, has a total of about 7 million ha of bamboo forest (Perez *et al*., 1999). Of these, over 30% is covered by the world's single most important bamboo species, *Phyllostachys pubescens* (Li and Xu, 1997). The area under bamboo in India has been estimated at between 3 and 10 million ha (Biswas, 1988; Fu and Banik, 1995) and that in Myanmar at 2.2 million ha (Fu and Banik, 1995).

The range of uses of bamboo for humans is remarkable, with an estimated annual use of 12 kg of bamboo products per capita in Asia (Recht and Wetterwald, 1988; Sastry, 1998). Besides some minor uses such as leaves for medical purposes (Zhang, 1997), fresh edible shoots, and culms for timber or as a raw material for pulping are the major products from bamboo. Data on worldwide production of bamboo products are extremely unreliable because they do not appear in the major commodity databases. Probably more than 2 million tons of bamboo shoots are consumed annually (Kleinhenz *et al*., 2000) with approximately 1.3 million t produced in China (Shi *et al*., 1997). Figures for timber will be multiple times greater, e.g., 3 million t/year in India (Subramanian, 1995), possibly more than 20 million t/year in China, and most likely about 30 million t/year worldwide. Total trade in bamboo products has been estimated at US$4.5 billion/year (Sastry, 1998). While supplying products of immediate use to humans, bamboo also serves multiple ecologic functions such as soil and water conservation, and erosion control (Fu and Banik, 1995). Due to its great potential for rapid biomass production (Pearson *et al*., 1994), bamboo is a significant net sink for global CO_2 (Jones *et al*., 1992).

Although vast land tracts in South and Southeast Asia are covered with bamboo, and area planted to bamboo is increasing in China by 51,000 ha/year (Li and Xu, 1997), there is rising concern about acute scarcity of bamboo products in the future (Hsiung, 1988). For example, in India it is projected that at the current level of bamboo productivity for the paper industry and with the growing demand for paper, an additional 30-60 million ha of land would be required by 2015 (Adkoli, 1991). Better resource use (Shende *et al*., 1998) and in particular suitable crop management practices (Yao, 1994; Fu and Banik, 1995; Perez *et al*., 1999) are given top priority to satisfy the anticipated increasing future demand for bamboo products.

This review aims to present an overview of the key aspects of the growth and development of bamboo, showing how they can be managed through agronomic techniques that enhance output particularly of edible shoots and timber. Emphasis is placed on the manipulation of standing-culm density, culm-age structure, leaf area, and leaf-age structure. Selected features of the impact of the environment, i.e., water availability and soil properties, on bamboo production are outlined, and approaches on how this environment can be managed, e.g., with irrigation, tillage, mulches, and fertilization, are discussed.

II. MANIPULATING GROWTH AND DEVELOPMENT IN BAMBOO

Bamboos (*Bambusoideae*) comprise a subfamily of the grasses (*Poaceae*). They are evergreen, monocotyledonous (i.e., nonwoody) plants which produce primary shoots without any later secondary growth. Each shoot has a distal aerial part called the culm, a proximal, ground-level part called the culm neck, and a subterranean part called the rhizome. Culms consist of nodes and internodes—the former with meristematic tissue from where culm sheaths and branches arise (Chua *et al*., 1996). Young culms with compressed internodes and including a part of the culm neck are harvested for edible shoots, weighing from 0.25 to 5.00 kg each depending on species. Mature culms provide timber that is put to multiple uses. Rhizomes as culms consist of nodes and internodes. According to their morphology, bamboos are broadly divided into monopodial (or "running") bamboos with "leptomorph" rhizome systems, and sympodial (or "clumping") bamboos with "pachymorph" rhizome systems. The internodes of leptomorph rhizomes are longer than broad, and lateral buds on nodes can produce either new shoots or other rhizomes. The internodes of pachymorph rhizomes are broader than long, and lateral buds on nodes produce only rhizomes (Valade and Dahlan, 1991). In sympodial bamboos, new culms develop from buds on elongated culm necks (pseudo-rhizomes) rather than from buds on rhizomes. These differences in rhizome system can be regarded as adaptations to the climatic conditions to which bamboos are native to: monopodial bamboos are native to temperate climates with cool, wet winters, and sympodial bamboos to tropical climates with a pronounced dry season. The tight-clumping habit of tropical species supposedly evolved from the leptomorph form of rhizomes and provides less rhizome surface to dehydrate during extended dry seasons (Farrelly, 1984).

That bamboo is "one of the fastest growing plants" is attributed to the speed of culm growth. This fast growth phase results from expansion of individual internodes and, depending on species, culms can grow to 3-30 m long within 3-4 months (Liese and Weiner, 1995; Chua *et al*., 1996). It is generally agreed that up to a certain age, height and diameter of the annual flush of culms increase (Londoño, 1992). Particular environmental conditions, such as higher temperature (Sun and Yang, 1988; Lan, 1990), greater water availability (Koyama and Uchimura, 1995), and higher air humidity (Farrelly, 1984) promote culm growth. Culms which emerge early in the season can fully develop during the warm summer in temperate climates and during the wet season in tropical climates, whereas "late" culms rarely survive into the second growing season due to cool-temperature conditions in temperate climates or to dry soil conditions in tropical climates (Pearson *et al*., 1994).

The culm tissue consists of about 50% parenchyma and 50% vascular bundles. The latter are composed of fibers (40%) and conducting tissue (10%). The conducting tissue consists of the xylem in the form of metaxylem vessels and the phloem in the form of sieve tubes (Liese, 1995). In contrast to culms which are <1 year old, parenchyma cells of culms which are 1 year and older can contain starch (Liese and Weiner, 1995). Earlier reports indicate that lignification of parenchyma cells proceeds over several years (e.g., 3-4 years; Yang and Huang, 1981). More recent studies, however, show that this process is essentially complete by the time their branches and leaves have fully expanded after one growing season (Itoh, 1990). At 1 year of age, bamboo culms have also already attained their maximum fiber content (Fu and Banik, 1995). Aging of culms is associated with significant chemical and structural changes in parenchyma and fiber tissues, which include decreases in moisture content (Espiloy, 1994; Sattar *et al*., 1994), cell wall thickening (Liese, 1995), decreases in percentage of holo- and α-cellulose (Chen *et al*., 1987) and sugars (Mohamad, 1995), accumulation of silicon (Fu and Banik, 1995), and increases or decreases in certain nutrient ions (Chen *et al*., 1987). In contrast to dicotyledonous plants, conducting tissues of bamboo have to function for many years without the formation of any new tissue (Liese, 1995). Furthermore, dicotyledonous trees can shed metabolic residue substances with their bark or deposit them in special tissues such as heart wood, but such substances accumulate in metaxylem vessels (e.g., tyloses and slime substances) and sieve tubes (e.g., callose) of bamboo culms (Liese, 1991). This progressively decreases the conductivity of the xylem for water and nutrients and that of the phloem for assimilates, and finally leads to the breakdown of the transport system and death of culms (Liese, 1995; Liese and Weiner, 1995). Culms of some species can have a life span of several decades. For example, Pearson *et al*. (1994) estimated a life span of 33 years for *Chusquea culeou*.

A. UPTAKE OF WATER AND NUTRIENTS

Absorption of water and nutrients from the soil by bamboo depends on the growth habit and functionality of their roots and rhizomes. With the exception of studies on the distribution of bamboo root biomass down the soil profile, little or no research has been conducted on more important root parameters such as root length density or efficiency of absorption of soil water and nutrients. As in any other plant species, the fine roots and root hairs of the bamboo root system play a significant role in supporting high productivity (Tripathi and Singh, 1996).

It is generally agreed that root systems of bamboo do not usually elongate to great soil depth but rather develop a profuse root mat of highly efficient fine roots and root hairs within the uppermost soil layer (Christanty *et al*., 1997). The root and rhizome system is usually confined to the topmost soil layer (the A and part of the B layer) with only a few roots extending below 40-cm depth. Qiu *et al*. (1992) determined that approximately 90% of the total belowground biomass of *P. pubescens* was within 60 cm of the surface. Li *et al*. (1998c) showed that 90% of the total belowground biomass of a >50-year old stand of *P. pubescens* was located in the topmost 30 cm with only thick (i.e., unproductive) roots and dead biomass below that depth. Huang (1986) found a very similar distribution of root and rhizome biomass for the same species. The author speculated that roots might only extend to a maximum of 1 m when the soil A horizon is very deep. Table I presents a summary of effective root zones for several species. Shallow root systems of bamboo are more prone to deficient and fluctuating soil-water conditions than deeper-located root systems of other plants, but they are less likely affected by overwet soil conditions to which they are susceptible (Farrelly, 1984). The topmost soil horizon is typically well aerated, and natural mineralization of nutrients is usually quicker there than in deeper layers. Plant-available ions are effectively and almost immediately absorbed by the dense root system of bamboo plants in this horizon, which explains their function to accumulate and sequester nutrients (Toky and Ramakrishnan, 1982) and their quick response to fertilization (Li *et al*., 1998c). Therefore, leaching of nutrients is very low in bamboo stands (e.g., 0.3-9.2, 0.07-0.3, 2.8-13.7 kg/ha/year of N, P, K) (Toky and Ramakrishnan, 1981; Mailly *et al*., 1997).

Table I

Vertical Location of Root and Rhizome Biomass in Bamboo

Bamboo species	Root and rhizome zone[a] (cm soil depth)	Reference
(in general)	0-30	Farrelly (1984)
Phyllostachys pubescens	0-30	Li *et al*. (1998c)
Phyllostachys pubescens	0-30	Wu (1984)
Phyllostachys pubescens	0-33	Oshima (1931a)
Phyllostachys pubescens	0-40	Qiu *et al*. (1992)
Phyllostachys pubescens	10-40	Huang *et al*. (1993)
Phyllostachys nidularia	30-40	An *et al*. (1995)
Phyllostachys fimbriligula	15-35	Cai and Wang (1985)
Chusquea sp.	0-30	Widmer (1998)
Chusquea culeou	20-30	Pearson *et al*. (1994)

[a] I.e., the soil layer where at least 80% of the total root and rhizome biomass is located

There is not much evidence to support the argument that greater soil depth promotes greater productivity in bamboo. In correlation analyses with *P. bambusoides,* surface soil depth was positively correlated with bamboo growth (Chung and Ramm, 1990). "Growth", i.e., biomass production, however, is not necessarily equivalent to yield: Zhang *et al*. (1996) measured greater stand biomass but lower timber yield in *P. nidularia* when the soil layer was deeper. This is due to the interaction between rhizome age and position of rhizomes down the soil profile: older rhizomes are generally deeper positioned. Due to the age of their tissues, buds on nodes of older rhizome parts are less effective in producing new shoots/culms. In the sympodial bamboo species *C. culeou*, development of buds into shoots was restricted to pseudo-rhizomes ≤ 4 years old (Pearson *et al*., 1994). For the monopodial species *P. pubescens*, buds on 3-4-year-old rhizomes tended to have the greatest potential for development into new shoots (Zhou *et al*., 1985). Rhizomes which are positioned deeper in the soil profile tend to produce only shoots of poor quality (Raghubanshi, 1994). Due to the longer time required for shoots to extend to the soil surface, these develop too late in the season to mature adequately during the short remaining growing season (Oshima, 1931b). From an economic perspective, belowground harvesting of shoots developing from older and deeper-positioned rhizomes is too labor intensive for viable production of fresh, edible bamboo shoots (Oshima, 1931b).

Figure 1a shows the typical variations in growth rates of rhizomes and roots for a monopodial bamboo in a northern-hemisphere temperate climate. New rhizomes develop from buds on nodes of older rhizomes in June and begin branching from August. Maximum rhizome growth occurs from July to September and is succeeded by growth of new roots, which develop from buds on those rhizomes during September-October. Due to low ambient temperatures during January and February and subsequent rapid growth of belowground shoots and aboveground culms until April/May, growth rates of rhizomes and roots remain low during this period. In sympodial bamboo, i.e., the "tropical" group, the drop in growth during January-February will either not be as pronounced or not occur at all. The efficiency by which roots absorb nutrients (and possibly water) varies with season as well: higher nutrient absorption rates in *P. pubescens* were measured during the shoot-emergence and subsequent culm-elongation phase (Fu *et al*., 1994).

B. PHOTOSYNTHESIS

In common with other crops, the total photosynthesis of bamboo stands is determined by the leaf area and by the photosynthetic capacity of the canopy. The photosynthetic capacity of an individual leaf depends on its age, its nutritional status (Section III.C), the age of the culm it is growing on, its position in the canopy, and on climatic conditions such as temperature and photon-flux density which vary with season. The photosynthetic capacity of the bamboo canopy is not only determined by the photosynthetic capacity of leaves as outlined above, but also depends on the life span of leaves which influences the leaf-age structure of its canopy. The life span of leaves is substantially different between monopodial and sympodial bamboos.

Understandably, the leaf area index (LAI) of a complete bamboo canopy increases with leaf biomass across bamboo species and ranges from 5 to 12 (Qiu *et al*., 1992; Huang *et al*., 1993; Isagi *et al*., 1993; Fang *et al*., 1998; Li *et al*., 1998a). It is generally recognized that photosynthetic activity of leaves steadily declines with age after full expansion. Huang (1986), Huang *et al*. (1989), and Qiu *et al*. (1992) noted photosynthesis rates up to three times higher in new (<1 year old) leaves compared with those of older (>1year old) leaves. For example, the net photosynthetic rate of new leaves (2 months old) was 2.5 times greater than that of 1-2-year-old leaves in *P. pubescens* (Huang, 1986). This was attributed to greater metabolic activity of tissues (Huang, 1986) and higher nutrient concentrations (Zhou and Wu, 1997) in younger leaves. A similar trend was found in other bamboo species; concentrations of N, P, and K in <1-year-old leaves of *Bambusa distegia* were 2.74%, 0.21%, and 1.68% whereas those in 1-year-old leaves were only 2.31%, 0.20%, and 1.30% (Zhou and

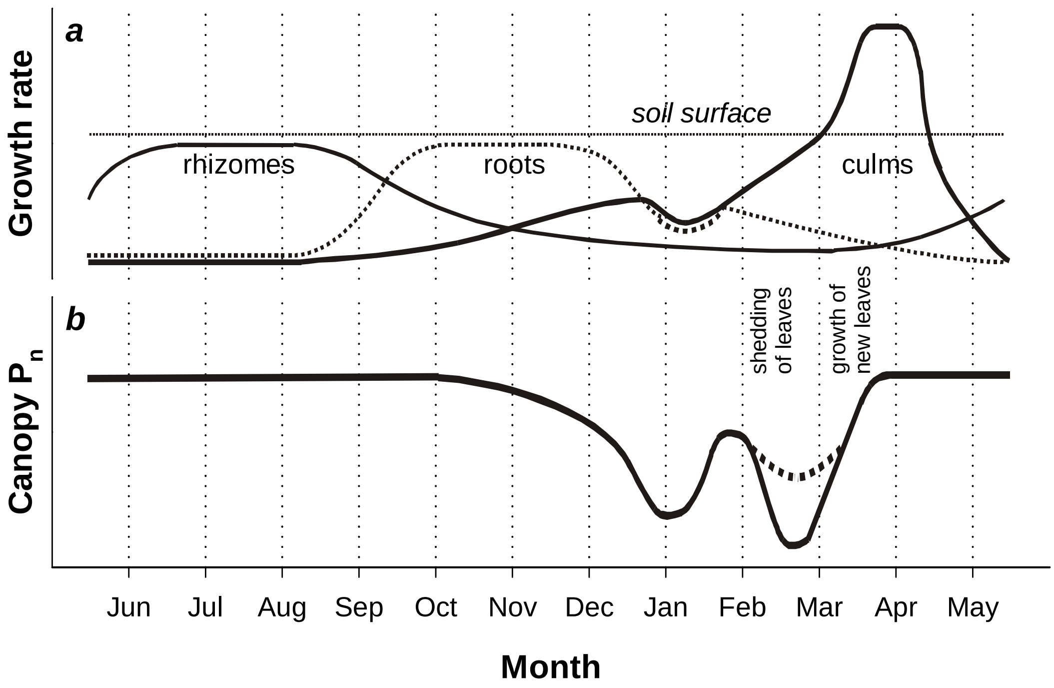

Figure 1 Annual cycle of (a) growth rates of aboveground and belowground plant parts, and (b) canopy photosynthetic rate of a typical monopodial bamboo in a temperate climate. The straight curve in the lower graph (b) indicates the canopy photosynthetic rate for an "alternating" monopodial bamboo in an "off year," and the dotted curve for an "alternating" bamboo in an "on year." Adapted from Dreckmann (1995). See text for details.

Wu, 1997). Higher content of nutrients such as N promotes development and prevents collapse of chloroplasts in leaves and is closely correlated with the photosynthetic rate of leaves (Mengel and Kirkby, 1987). Shanmughavel *et al.* (1997) found that the concentration of chlorophyll in 1-year-old leaves was 1.5 times greater than that in 6-year-old leaves of *B. bambos*. This was associated with 30% greater concentrations of carotenoides, protein, and starch in younger leaves.

The photosynthesis rate of bamboo leaves not only depends on their age, but also independently on the age of the culm upon which they are found. In young (≤ 7-8 years old) bamboo stands, leaves on older culms are shaded more than those on younger ones since younger culms are taller then older culms until the stand reaches its maximum height. In mature (>7-8 years old) stands, transmission of light decreases rapidly from the top of the bamboo canopy towards the bottom (Yang *et al.*, 1988). In studies conducted by Qiu *et al.* (1992), only 5% of the light present at the top of the canopy penetrated to the leaves at the bottom of the canopy of *P. pubescens*. Unpublished data from Kleinhenz and Midmore confirm that the photosynthetic capacity of leaves depends on the age of culms they are growing on. Photosynthesis was measured in leaves of the same age (youngest, fully expanded) on culms of up to 4 years old. The photosynthetic rate of leaves decreased significantly with age of culms. This may be closely related to reduction in the supply to leaves of water and nutrients to sustain high photosynthetic rates when culms age, and the conductivity of metaxylem vessels decreases.

Diurnal changes in air temperature and photon-flux density and seasonal variation in both especially for bamboo found in temperate zones have marked effects on leaf photosynthesis. During January and February, the photosynthetic rate of leaves is low due to low air temperature (Huang *et al*., 1989; Koyama and Uchimura, 1995; Fig. 1b). In studies conducted by Koyama and Uchimura (1995) with *P. bambusoides*, net photosynthesis increased until air temperature was 27°C, but decreased rapidly thereafter. The compensation point at which the respiration rate equals that of photosynthesis was a little below 40°C. Net photosynthesis rates (P_n) reached saturation at 12 µmol $CO_2/m^2/s$ when the PAR was 1,200 µmol/m^2/s. Therefore, P_n in *P. bambusoides* peaked around midday. It is probable that “critical” levels especially of temperature and perhaps of PAR will be much higher for tropical and typically sympodial bamboo.

Another fundamental difference between monopodial and sympodial bamboo is the life span of their leaves. The life span of leaves of monopodial bamboo is no more than 2 years (Hong, 1994; Li *et al*., 1998c) whereas that of leaves of sympodial bamboo can extend to about 6 years (Pearson *et al*., 1994; Shanmughavel *et al*., 1997). The leaf-age structure of canopies also differs between monopodial and sympodial bamboo. In monopodial bamboo, leaf age on culms of a specific age is very similar, whereas in sympodial bamboo it varies greatly. The life span of leaves of monopodial bamboos on culms ≤1 year old is 1 year, while that of leaves on culms >1 year old is 2 years (Table II). The low leaf area of culms <1 year old cannot sustain the demand for photosynthates for its own growth. One-year-old leaves have a high photosynthetic capacity, but they are shed just before young bamboo shoots extend through the soil surface. Leaves on culms of “even-year” age are 1 year old and have high photosynthetic capacity, whereas those on culms of “uneven-year” age are 2 years old and are shed just before new shoots emerge aboveground. As long as a stand of monopodial bamboo is composed of an equal number of adult culms of “even” and “uneven” age, there will be no differences in productivity between subsequent years (Li *et al*., 1998c). If for any reason (e.g., uncontrolled logging or destructive weather conditions), however, the ratio between number of adult culms of “even” age and those of “uneven” age becomes unequal to 1, the bamboo stand will have relatively more culms with 1-year-old leaves in 1 year and relatively more culms with 2-year-old leaves in the next. In years when there are more culms with 1-year-old leaves, there is only little reduction in canopy photosynthetic rate when the (comparably fewer) 2-year-old leaves are shed (Fig. 1b). There is, therefore, sufficient energy available to sustain culm production of monopodial bamboos. In years when there are more culms with 2-year-old leaves, however, leaf area and canopy photosynthetic rate are significantly reduced when those leaves are shed (Fig. 1b). Less energy becomes available for development of new shoots and, therefore, productivity is low (Li *et al*., 1998b). This biennial life span of leaves and the imbalance between “even” and “uneven” age structure of culms cause the long-known phenomenon of alternation (i.e., large differences in productivity between years) in monopodial bamboos (Hong, 1994; Li, 1998). The belief that the biennial alternation in growth between above- and belowground plant parts is a result *per se* of formation of more shoots in 1 year and formation of more rhizomes in the next has not been proven (Cheng, 1983; Liao, 1984; Liao, 1988).

There is much less information available on the life span of leaves of sympodial bamboo species. The life span of leaves of *B. bambos* is at least 6 years (Shanmughavel *et al*., 1997). Pearson *et al*. (1994) recorded the survival of leaves of *C. culeou*; the average life span of leaves of this sympodial species was 2-5 years with

Table II

Characteristics of Leaves, Recorded Just Before the Shoot Season, on Culms of Different Age in *P. pubescens*

Culm age (years)	Leaf characteristics
<1	<1-year old, high photosynthetic capacity, low leaf area[a]
1	1-year old, high photosynthetic capacity, shed before shoot emergence
2, 4, 6, 8…	1-year old, high photosynthetic capacity
3, 5, 7, 9…	2-year old, low photosynthetic capacity, shed before shoot emergence

Note. Adapted from Hong (1994) and Li *et al*. (1998c)
[a] Recorded at the end of shoot season

only a few surviving 6 years. Due to the longer and variable life span of leaves, shedding of leaves is more evenly distributed between leaf and culm ages in sympodial than in monopodial bamboos, thus alleviating alternation in total leaf area, photosynthetic output, and productivity between years. In bamboos in tropical climates, the drop in photosynthesis rate during January and February is not as pronounced as for bamboos in temperate/cold climates or it is nonexistent. Some tropical sympodial bamboo species, however, expand leaves on newly emerged culms much later than the normal April-May period (Pearson *et al*., 1994). Therefore, potential canopy photosynthesis may be restricted in those species for a longer time, coinciding with the development of new rhizomes and subsequently, roots.

Although sympodial bamboos are less affected by biennial variations in photosynthetic rate, they are more affected by loss of photosynthetic capacity of the canopy over time. And although there is unlikely to be a difference in the viability of culm tissues (i.e., loss of conductivity of metaxylem and sieve-tube tissues) during aging between sympodial and monopodial species, the canopy of monopodial species is rejuvenated every year when 2-year-old leaves are replaced by new ones. Those of sympodial species remain on culms longer. Therefore, culms of sympodial bamboo older than 2 years contain relatively older and less productive leaves than monopodial bamboo, reducing the inherent photosynthetic capacity of their canopies. In addition, especially in mature canopies, there is much greater self-shading of younger leaves by older leaves than in monopodial bamboo.

C. Storage and Translocation of Photosynthates and Nutrients

For growth and production of commercial bamboo, it is particularly important to know the sources of energy and nutrients that sustain the rapid accumulation of biomass in young culms. Since shoots and later young culms have essentially no photosynthetic leaf area to provide energy and sustain their growth, net-import of energy is required at least for their early growth (Pearson *et al*., 1994; Liese, 1995). Until recently, it was thought that bamboo rhizomes store the greater part of that large amount of energy required (Farrelly, 1984; Liese, 1985). Li *et al*. (1998c), however, estimated that during the rhizome growth stage (Fig. 1a) only 26% of the total nonstructural carbohydrates in *P. pubescens* was located in rhizomes whereas culms contained 44%. Both Uchimura (1980) and Li *et al*. (1999) measured decreases in concentration of carbohydrates in rhizomes during new culm and rhizome growth in the same species, but the latter calculated that the decrease in carbohydrate content of rhizomes could have provided no more than 20% of the carbohydrates required for the accumulation of biomass in new and nonphotosynthesizing culms. There was no significant reduction in carbohydrate content *per se* in leaves of older culms either and, therefore, it was concluded that the remaining 80% most likely originated from current photosynthesis and stored photosynthates in older (≥1-year-old) culms. This hypothesis was supported by Liese and Weiner's (1995) review, which shows that in contrast to culms of less than 1 year old, culms 1 year and older can contain starch. Sulthoni (1995) studied seasonal variations in starch contents of bamboo culms of *B. vulgaris*, *Dendrocalamus asper*, *Gigantochloa apus*, and *G. atter*. Their starch contents were high before the shoot season (i.e., the period when shoots extend through the soil surface), but were nonexistent after completion of culm expansion (Sulthoni, 1995). That starch is not stored in those culms thereafter until just prior to the next shoot season suggests that photosynthesis by culms ≥1 year old after the shoot season does not contribute to the storage of nonstructural carbohydrates in readiness for the following shoot season but rather to development of new rhizome and root biomass.

Qiu *et al*. (1986) labeled culms of *P. pubescens* after the shoot season with ^{32}P to measure its translocation to other plant parts. For 2 days, there was no export from the labeled culm but from then on for 2 months, ^{32}P was increasingly translocated through the rhizome into above- and belowground plant parts of other culms. There was greater translocation into leaves and bases of culms compared with other plant parts. Less ^{32}P was translocated to more distant culms, which explains why growth of new shoots and culms is better when distance to older sustaining culms is minimal (Li *et al*., 1998a). Since the distance between older culms and new culms increases (Valade and Dahlan, 1991) and conductivity of transporting tissues in older culms is less effective (Liese, 1991), the ability of older culms to translocate photosynthates into new culms decreases with their age. Taken together these results suggest that there is no "true" storage of photosynthates in bamboo. Assimilation products are temporarily stored in culm tissues (i.e., parenchyma cells) to be remobilized and translocated to rapidly growing new culms (and other plant parts) as needed. The primary role of (pseudo-) rhizome tissues in bamboo is transport rather than storage, i.e., to connect young culms dependent upon imported carbohydrates to older culm sources.

Although bamboo rhizomes may contain large quantities of nutrients (e.g., 196, 8, 93 kg/ha N, P, K; Li *et al*., 1998c), their ability to remobilize and translocate these to new culms (and other plant parts) is questionable. Li *et al*. (1999) noted no decrease in nitrogen content in rhizomes over the shoot season, indicating that N supply of new culms from N stored in rhizomes was insignificant or that export of stored N from rhizomes was adequately replaced by N from other plant parts or from the soil. In the same study, the authors calculated that translocation of nutrients from remobilized reserves in other plant parts (e.g., senescing leaves) was only of minor significance (e.g., 7% of N required). They, therefore, concluded that required nutrients to sustain the rapid growth of culms were mainly absorbed directly from the soil.

The seasonality of uptake, storage, and translocation of photosynthates and nutrients directly impacts on scheduling of culm harvest for timber which should not be performed just prior to or during the shoot season (Farrelly, 1984; Siddiqui, 1994; Sulthoni, 1995). Additionally, since culms contain starch during this period, if harvested at this time they will be more vulnerable to insect attacks, which lowers timber quality (Sulthoni, 1995). Another argument for harvesting mature culms during the off-shoot season is that plant sap flow rates and, therefore, loss of plant sap and nutrients through cut stumps, is minimal during this season (Zhang *et al*., 1994; Huang and Wang, 1996).

D. Accumulation and Partitioning of Biomass and Nutrients

Farrelly (1984) defined bamboo growth as the annual development of an increasing number of thicker and taller culms "until the maximum stature and productivity for the species is reached under specific local conditions of weather and soil fertility." When bamboo is left undisturbed after planting, i.e., no shoots or culms are harvested, the annual biomass production rate is characterized by a sigmoid increase until 3-5 years (Fig. 2). Once the number of (mature) culms reaches a certain limit, congestion of below- and aboveground plant parts occurs (Oshima, 1931b; Kondas, 1981). Due to lack of growing space, growth of new rhizomes and culms physically interferes with mature rhizomes and culms (Kigomo and Kamiri, 1985) and an increasingly greater proportion of new culms will be malformed, will break, or will die during expansion (Prasad, 1987). This results in stagnation of annual growth, and rates decrease during later growth.

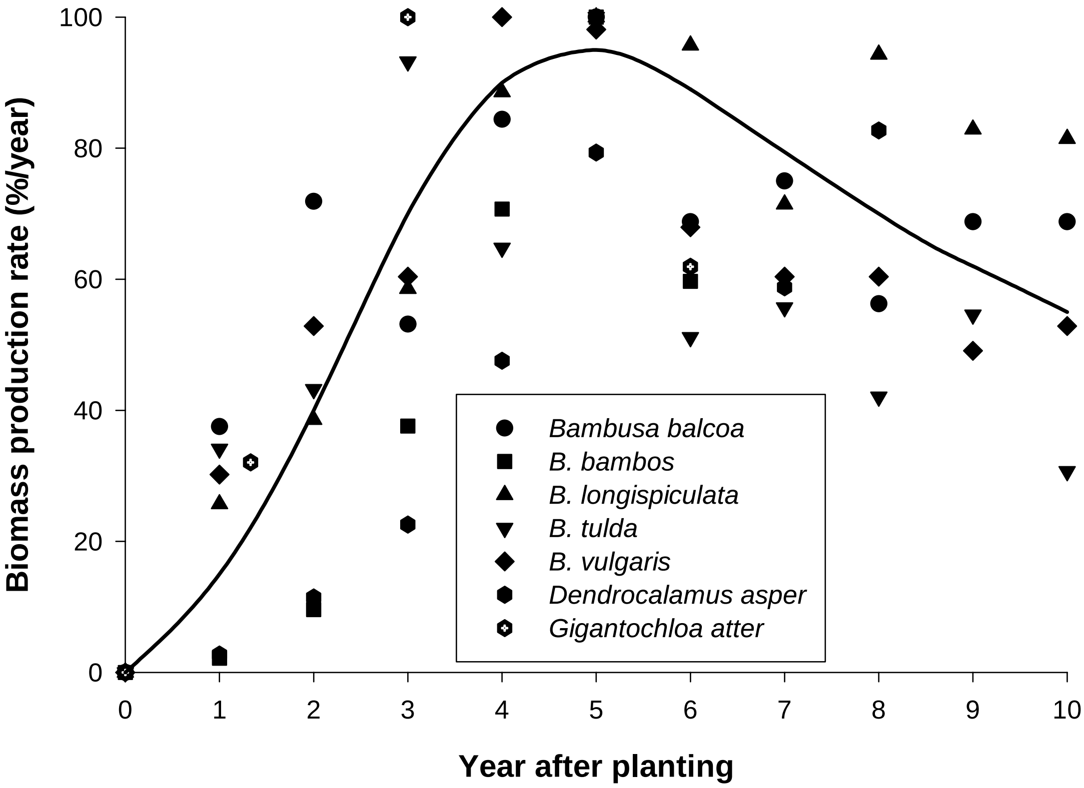

Figure 2 Relative biomass production rates of several bamboo species as affected by age of stands. Adapted from data published in Banik (1988), Kao and Chang (1989), Christanty *et al*. (1996), and Shanmughavel *et al*. (1997).

Table III presents an overview of biomass accumulation in several bamboo species. Although there is great variation in stand biomass between species and between studies (essentially environments) within the same species (e.g., *P. pubescens*), the overall range in total biomass between monopodial and sympodial bamboo species was

Table III

Biomass and its Partitioning in Several Bamboo Species

	Biomass (t/ha)									
	Aboveground				Belowground					
Bamboo species	Culm	Branches	Leaf	Total	Rhizome	Roots	Total	Total	Comments	Reference
Monopodial species										
Phyllostachys bambusoides	93	10	9	112	33	15	48	160	natural stand	Isagi *et al*. (1993)
Phyllostachys nidularia	38	—[a]	—	56	—	—	—	—	extensively used	Zhang *et al*. (1996)
Phyllostachys pubescens	117	16	6	139	17	28	45	184	natural stand	Isagi *et al*. (1997)
Phyllostachys pubescens	—	—	—	129	—	—	53	182	annual culm harvest; "good site"	Huang *et al*. (1993)
Phyllostachys pubescens	—	—	—	58	—	—	62	120	annual culm harvest; "poor site"	Huang *et al*. (1993)
Phyllostachys pubescens	—	—	—	40	—	—	80	120	annual culm harvest	Sun *et al*. (1986)
Phyllostachys pubescens	49	10	3	62	31	31	70	132	extensively used	Li et al. (1998c)
Phyllostachys pubescens	—	—	—	59	—	—	57	116	annual culm harvest	Qiu *et al*. (1992)
Sympodial species										
Bambusa arundinaceae	—	—	—	83	—	—	—	—	4 years after planting	Groulez, 1966
Bambusa bambos	243	40	4	287	—	—	11	298	6 years after extensive use	Shanmughavel *et al*. (1997)
Bambusa blumea	—	—	—	143	—	—	—	—	extensively used	Uchimura, 1978
Bambusa vulgaris	—	—	—	106	—	—	—	—	extensively used	Uchimura, 1978
Chusquea culeou	—	—	—	158	—	—	—	—	natural stand	Veblen *et al*. (1980)
Chusquea culeou	—	—	—	130	—	—	50	180	natural stand	Pearson *et al*. (1994)
Chusquea tenniflora	—	—	—	13	—	—	—	—	natural stand	Veblen *et al*. (1980)
Dendrocalamus strictus	8	—	1	9	—	—	—	—	4 years after clear felling	Joshi *et al*. (1991)
Fargesia denudata	—	—	—	11	—	—	12	23	food source for Panda	Wang and Ma (1993)
Fargesia scabrida	—	—	—	9	—	—	—	—	food source for Panda	Taylor and Qin, 1987
Fargesia spathacea	—	—	—	24	—	—	—	—	food source for Panda	Taylor and Qin, 1987
Gigantochloa atter	34	6	5	45	11	21	32	77	6 years after clear felling	Mailly *et al*. (1997)
Schizostachym lumampao	—	—	—	66	—	—	—	—	extensively used	Uchimura, 1978
Sinarundia fangiana	—	—	—	7	—	—	—	—	food source for Panda	Taylor and Qin, 1987
Sphaerobambos philippinensis	112	16	37	165	—	—	—	—	4 years old; flat land	Virtucio *et al*. (1996)
Sphaerobambos philippinensis	25	5	11	41	—	—	—	—	4 years old; hill land	Virtucio *et al*. (1996)
Thyrostachys siamensis	—	—	—	54	—	—	—	—	"good" site	Suwannapinunt (1983)
Thyrostachys siamensis	—	—	—	11	—	—	—	—	"poor" site	Suwannapinunt (1983)

[a] No information provided

essentially similar. Total biomass in both bamboo types averaged 145 t/ha. Jones *et al*. (1992) concluded that the primary production of a bamboo forest in Thailand was comparable to that of other tropical grasslands, Ma *et al*. (1994) found that bamboo biomass was identical with that of bush land, and Isagi (1994) highlighted the fact that bamboo forests act, therefore, as significant sinks for carbon. Accumulation of biomass in monopodial and sympodial bamboo is essentially the same. Monopodial species, however, partition more of their biomass into belowground organs, and within belowground organs, they partition more biomass into rhizomes compared with sympodial species. On average, belowground biomass is higher for monopodial species (43% of total biomass) than for sympodial species (31% of total biomass). There appear to be only small differences in partitioning of aboveground biomass: allocation to culms, branches, and leaves was 82%, 12%, and 6% in monopodial bamboos and 77%, 13%, and 10% in sympodial bamboos. Differences were greater belowground, with 54% and 46% of belowground biomass allocated to rhizomes and roots in monopodial species, and 34% and 66% in sympodial species. Bamboo grown under poorer soil conditions accumulates less total biomass but relatively more biomass is allocated to belowground plant parts.

Biomass can vary substantially within individual species, even when cultivated at the same site. Due to their high genetic variability, species of *Dendrocalamus* such as *D. latiflorus* are notorious for such differences. Although *D. latiflorus* may have a yield potential of up to 41 t/ha of edible shoots per year (Pan, 1986), Lü *et al*. (1997) found great variations in growth between plants. Kiang *et al*. (1976) measured yields of edible shoots ranging from 7.4 to 20.3 kg/clump/year in different strains of *D. latiflorus* growing in one site.

Table IV presents an overview of reported accumulation and partitioning of the major plant nutrients N, P, and K. Average total accumulated N, P, and K in bamboo was 288, 44, and 324 kg/ha; thus the N:P:K ratio was 7:1:7. Nutrient content of culms (151:32:265 kg/ha N:P:K) averaged higher than that of rhizomes (115:10:73 kg/ha N:P:K), supporting the argument that rhizomes are not a primary storage organ for nutrients (Section II.C). Due to the low biomass of branches (Table III), their nutrient content is similarly low (10-13% of total content of N, P, and K). Although leaves represent only 7-10% of total plant biomass, their high nutrient concentration makes them a major sink for nutrients, representing 37%, 23%, and 20% of total N, P, and K in bamboo. The aboveground plant parts and particularly culms (N:P:K ratio: 5:1:8) contain more K, whereas belowground parts and particularly rhizomes (N:P:K ratio: 12:1:7) contain more N. Within aboveground plant parts, relatively more N is allocated to leaves (N:P:K ratio: 11:1:7).

E. Management of Bamboo Growth

Manipulation of culm growth in bamboo involves the removal (i.e., harvesting) of culms of different age. Bamboo may be grown solely for one or more products at the same time. Thus, culm management aims to maximize the yield of one product, or alternatively to optimize yield of individual products to increase their combined monetary output. Since bamboo is a perennial, all culm management practices must also aim to sustain long-term productivity of the stand (Virtucio, 1996). The intensity of removal dictates the total number of culms per unit area remaining, and the choice of culms harvested based upon maturity status governs the age structure of culms (i.e., the relation between younger culms and older culms).

Table IV

Accumulated Nutrients and their Partitioning in Several Bamboo Species

	Nutrient content (kg/ha) and concentration (%)							
	Aboveground				Belowground			
Nutrient and bamboo species	Culm	Branches	Leaf	Total	Rhizome	Roots	Total	Total
Nitrogen								
Dendrocalamus strictus[a]	0.66%	0.91%	2.27%	—[f]	0.47%	1.01%	—	60
Gigantochloa atter[b]	55	19	57	131	33	87	120	251
Phyllostachys pubescens[c]	124	58	92	274	196	82	278	552
Sphaerobambos philippinensis[d]	348	58	213	619	—	—	—	—
Sphaerobambos philippinensis[e]	78	18	62	158	—	—	—	—
Phosphorus								
Dendrocalamus strictus[a]	0.17%	0.19%	0.39%	—	0.11%	0.08%	—	15
Gigantochloa atter[b]	38	7	9	54	12	23	35	89
Phyllostachys pubescens[c]	9	3	5	17	8	2	10	27
Sphaerobambos philippinensis[d]	67	11	19	97	—	—	—	—
Sphaerobambos philippinensis[e]	15	3	6	24	—	—	—	—
Potassium								
Dendrocalamus strictus[a]	0.84%	0.98%	1.92%	—	0.41%	0.43%	—	70
Gigantochloa atter[b]	193	39	45	277	53	90	143	420
Phyllostachys pubescens[c]	221	39	29	289	93	100	193	482
Sphaerobambos philippinensis[d]	528	47	145	720	—	—	—	—
Sphaerobambos philippinensis[e]	119	14	45	178	—	—	—	—

Note. [a] 2-year old stand, no data for biomass of individual plant parts; [b] 4-year old stand; [c] >50-year old stand; [d] 4-year old stand, flat land; [e] 4-year old stand, hill land

[a] Joshi *et al*. (1991)

[b] Mailly *et al*. (1997)

[c] Li *et al*. (1998c)

[d] [e] Virtucio *et al*. (1996)

[f] No information provided

1. Age of Harvested Culms

Culm age is tremendously important for quality of harvested bamboo products. Culinary bamboo shoots are immature culms harvested when <1 year old. They are harvested just prior to or shortly after emergence. Fibers develop in internal shoot tissues (Liese and Weiner, 1995) and harvesting shoots late lowers their culinary quality. For pulping and papermaking, 1-year-old bamboo culms are harvested when fiber quality is superior to that of older culms (Fu and Banik, 1995). While timber quality of culms of some species such as *P. pubescens* improves with increase in cell-wall density until 6-7 years (Huang *et al*., 1993), culms of most bamboo species "mature" and can be harvested after 3-4 years. At this stage, they have attained their maximum static bending and compression strength (Huang *et al*., 1993; Espiloy, 1994; Liese and Weiner, 1995), physical properties that usually deteriorate beyond that age.

2. Standing-Culm Density

In annual crops, occupation of space by plants is expressed as "planting density" or "planting population." This measure is unsuitable for bamboo since number of culms per plant can compensate dramatically for low plant populations. Moreover, due to the expansive nature of their rhizomes it can be difficult to identify individual plants in a stand of monopodial bamboos after only a few years. Therefore, "density" in a bamboo plantation is commonly expressed as "standing-culm density" although reference to the establishment of new stands is made based on planting density (Dart, 1999) largely because of stand establishment costs. Understandably, culm density can be the same for a plantation with lower planting density but higher number of culms per plant, and a plantation with higher planting density but less culms per plant (Siddiqui, 1994). The effects of standing-culm density on bamboo production vary considerably with bamboo species, age of bamboo stand, desired product and product quality, and site characteristics.

Optimum standing-culm density varies with bamboo species and is usually much higher for smaller-diameter species such as *P. nigra* and *P. nidularia* (about 1-4 cm diam. and 25-50,000 culms/ha; Shen *et al*., 1993; Zhang and He, 1997) than for medium-diameter species such as *P. makinoi* (about 4-5 cm diam. and 7-10,000 culms/ha; Yang and Huang, 1981), and bigger-diameter species such as *P. pubescens* (about 8-18 cm diam. and 3-5,000 culms/ha; Yang and Huang, 1981; Zhou *et al*., 1981; Liao, 1986; Dart, 1999).

In young plantations or in plantations that have been rehabilitated, e.g., by clear felling, (re-)growth tends to be more vigorous when the number of standing culms planted or not felled is greater (Mathauda, 1960; Tomar, 1963; Sutiyono *et al.,* 1989). This trend may be reversed, however, when bamboo plantations age. In studies by Fu *et al*. (1991a) with *P. pubescens* and Chen (1993) with *D. latiflorus*, stands with lower standing-culm density (1,500 culms/ha for *P. pubescens* and 875 culms/ha for *D. latiflorus*) yielded less shoots initially but surpassed yields of stands with greater standing-culm density (3,000 culms/ha for *P. pubescens* and 1,429 culms/ha for *D. latiflorus*) thereafter. Since standing-culm densities were fixed, this must have been due to increasing belowground competition (Section II.D).

One of the most important quality parameters in fresh bamboo shoots and culms for timber is diameter. There is an inverse relationship between yield and diameter of shoots and culms, which is determined by standing-culm density (Sagwal, 1987). As for the earlier mentioned relationship between standing-culm density and culm diameter of different bamboo species, lower standing-culm densities promote diameter but reduce total yield. On the other hand, high standing-culm densities increase total yield but reduce diameter of shoots and culms. For example, Fu and Banik (1995) recommended standing-culm densities of 1,500, 2,300, and 3,000 culms/ha for annual timber yields of <3.5, 3.5-7.0, and 7-10 t/ha in *P. pubescens.* Hu (1988) recommended standing-culm densities of 1,800-3,300, 10,500-12,000, and up to15,000 culms/ha for production of big-, medium-, and small-sized fresh bamboo shoots in the same species. It is apparent, however, that yield and diameter peak at different standing-culm densities. Yield and diameter usually increase with increasing culm density at low-density levels, peak at a range of optimum culm densities, and decrease thereafter. If density is quantified as the number of new shoots or culms produced per existing culm, it is apparent that relative productivity (and "relative" quality) diminishes with increasing culm density (Liao and Huang, 1984).

Optimum standing-culm densities for individual species also vary with growing conditions. Using data from a survey of commercial bamboo forests of *P. pubescens* and *P. makinoi* in Taiwan, Yang and Huang (1981) showed that growers maintain greater standing-culm densities under "poorer" conditions to promote higher culm yields, and lower standing-culm densities under "richer" conditions to promote greater culm diameter. The same is true for *D. strictus*: Siddiqui (1994) and Shi *et al*. (1993) recommend standing-culm densities of 1,700-1,900 culms/ha under "standard" conditions, but Patil *et al*. (1994) suggest a standing-culm density of 15-21,000 culms/ha on marginal land. Table VI presents the range of standing-culm densities across different bamboo species for various uses, and, where available, data on yield at those densities. Standing-culm densities vary according to factors mentioned: densities are lower for larger-diameter species, richer sites and under less intensive cultivation (i.e., semiwild stands). According to bamboo product, standing-culm density follows a sequence: shoots (7,400 culms/ha) < shoots and timber (9,100 culms/ha) < timber (13,300 culms/ha). There is, however, no notable difference in average standing-culm density between monopodial (10,300 culms/ha) and sympodial (10,400 culms/ha) bamboos in the range of standing-culm densities reported.

Inappropriate or inadequate culm management jeopardizes bamboo resources worldwide (Yao, 1994; Fu and Banik, 1995; Perez *et al*., 1999). These can result in two extremes: depleted stands with too few culms and overcrowded stands with too many culms. Unregulated exploitation of bamboo stands (i.e., overharvesting, especially of young culms) has depleted stands and resulted in declining supply of timber, e.g., in the Philippines (Virtucio and Tomboc, 1994) and in Indonesia (Sutiyono, 1988). This depletion is particularly serious in India where whole industries (cottage, agriculture, pulp and paper) depend on bamboo supply (Prasad and Chadhar, 1988; Patil *et al*., 1994). Curiously, congestion of stands in India's bamboo forests has also been attributed to unregulated overharvesting; when culms are heavily and irregularly harvested and conveniently removed only from the periphery of clumps, clumps become congested in the middle leading to a greater proportion of dead, broken, and malformed culms unsuitable for industrial use (Chaturvedi, 1988; Prasad and Chadhar, 1988). Congestion of clumps stresses bamboo plants to the extent that they may flower and finally die. Dwivedi (1988) showed that in contrast to well-managed and noncongested clumps of *D. strictus*, 36% more plants flowered and died when they were not properly managed and, therefore, congested. It has been proposed that clear felling and control of density of subsequent culm regrowth form the basis of a strategy for rehabilitating overharvested and congested clumps (Prasad, 1987; Prasad and Chadhar, 1988). Even simple management practices such as removal of dead and dying culms increased productivity of congested clumps (Sharma, 1980; Lakshmana, 1994b).

Table V

Litter Biomass and Nutrient Release in Several Bamboo Species

Bamboo species	Bamboo biomass (t/ha)	Annual litter biomass (t/ha/year)	Litter as % of bamboo biomass	Litter nutrient concentration (%)			Annual nutrient release (kg/ha/year)			Reference
				N	P	K	N	P	K	
Bambusa bambos	298	17.8	6	0.83	0.07	0.76	148	13	135	Shanmughavel and Francis (1997)
Dendrocalamus strictus	8	0.5	6	1.19	0.24	0.51	5	1	2	Joshi *et al*. (1991)
Dendrocalamus strictus	35	2.7	8	1.04	0.05	0.44	28	1.3	12	Tripathy and Singh (1994), Tripathy and Singh (1995)
Gigantochloa atter	77	4.7	6	1.21	0.69	0.96	57	9	45	Christanty *et al*. (1996), Mailly *et al*. (1997)
Sphaerobambos philippinensis	165	12.6	8	0.61	0.05	0.11	77	6	14	Virtucio *et al*. (1996)

3. Age Structure of Standing Culms

The age structure of a bamboo stand can be modified by felling culms when they have reached a specific age or by varying the length of the “felling cycle.” Imposing a felling cycle is not a culm-management practice *per se* but a modification of standing-culm density, culm-age structure, and also an indirect manipulation of the leaf-age structure of a bamboo stand. A long felling cycle allows culms to remain longer in a bamboo stand, thus increasing the proportion of older to younger culms and creating an older age structure. If culms are removed according to a short felling cycle, there will be a greater proportion of younger culms in a stand and, therefore, the age structure of the stand is younger. A too old or too young age structure of a stand may constrain stand productivity through decreases in the photosynthetic capacity of the canopy or in the photosynthetic active leaf area, respectively.

Age structure of standing culms is not a growth-limiting factor or a major consideration when the stand age is young. Young plants have a low leaf area index and total leaf area is the growth-limiting factor. Thus, a greater number of culms increases total leaf area, capture of solar radiation, and productivity in stands without full canopy closure. For maximum biomass production of a young stand, Thanarak (1996), and Tuncharearn and Suwajittanon (1996) recommend not harvesting culms in *D. asper* until a stand age of 4 years. In older plantations, ground cover by canopies is complete, and the photosynthetic capacity of leaves and the ability of culms to transport assimilates and nutrients limits growth. In sympodial bamboo, younger culms contain relatively younger and more productive leaves and their transporting tissues are more effective than older culms. This is substantiated by Chang and Junag (1985) who related yield of bamboo plantations of different age (2-6 years old) in Taiwan to the number of 2- and 3-year-old culms. The study shows that at a young plantation age, productivity depends more on older culms and when the plantation matures, comparably more on younger culms.

The optimum standing-culm density and age structure for maximum productivity of mature bamboo plantations is of foremost interest. A few studies have related productivity (i.e., shoot and timber yield, and number of new culms) of bamboo to the age structure of their stands. Lakshmana’s (1990) work with *B. arundinacea* showed that 1-year-old standing culms contributed 77% to annual production of new culms, 2-year-old standing culms, 20%, and standing culms >2 years old, only 3%. A similar contribution across age structure can be calculated with data from other studies, e.g., Huang (1984) with *P. pubescens*, Shanmughavel *et al*. (1997) with *B. bambos*, Kao and Chang (1989) with *D. asper*, and Prasad (1987) with *D. strictus*. It is apparent that younger culms contribute disproportionally in favor of production. In ancient China overharvesting of 1-year-old culms for papermaking harmed bamboo populations (Fu and Banik, 1995), while harvesting of 2-year-old culms resulted in depleted bamboo stands in Indonesia (Sutiyono, 1988). For many sympodial bamboo species in India, Chaturvedi (1988), however, concluded that culms >2 years old contribute only little to growth of new culms. It appears that 1-2-year-old culms are required to maintain productivity of bamboo stands; culms younger than 2 years must be left to reach productive age, while older culms could be harvested since they contribute little to stand productivity. Table VII presents an overview of reported age structure of standing culms in stands of several bamboo species. The average felling age for monopodial bamboo is 5-6 years, whereas that of sympodial bamboos is only 4 years. This is because the photosynthetic capacity of culms of monopodial bamboo is sustained longer as new leaves replace old leaves on a 2-year cycle and, therefore, they contribute more to growth of new shoots and culms than leaves of older culms of sympodial bamboo. In addition, culms of some monopodial species such as *P. pubescens* may be left standing for a later harvest since the quality of their timber improves until 6-7 years of age (Huang *et al*., 1993). Overall, for monopodial bamboo there are no differences in age structure of standing culms when it is grown either for fresh shoots or for culms as timber; about 40% of culms are 1-2 years old, 35% are 3-4 years old, 21% are 5-6 years old, and 3% are 7-8 years old. Consequently, management of standing-culm density (Section II.E.2) is a much more significant practice to manipulate bamboo growth for a required product than management of standing-culm age structure.

The primary cause for alternation in monopodial bamboo species is the lack of canopy photosynthesis due to reduction in total leaf area in "off years" when plants shed their 2-year-old leaves. In contrast to "standard" culm management where culms are annually felled, a single biennial felling cycle with no new shoots and culms removed in an "off year," is suitable to alleviate alternation in monopodial bamboos (Cheng, 1983; Qiu, 1984; Anonymous, 1986; Hong, 1994; Ma *et al*., 1996). The practice increases the photosynthetic capacity of bamboo stands over the longer term by increasing total leaf area and photosynthetic capacity of leaves through higher standing-culm density and lower culm-age structure (Zheng *et al*., 1996a). Zhang (1994) has developed a "cutting plan" that records and rationalizes density and age structure of standing culms in *P. pubescens* in an effort to improve bamboo production.

III. MANAGING THE ENVIRONMENT FOR BAMBOO PRODUCTION

A. WATER

Precipitation affects distribution and limits growth of bamboo more than any other component of climate, except temperature (Biswas, 1988). It has been reported that the minimum water requirement for cultivation of *D. asper* in Thailand is 1,000 mm/year (Thanarak, 1996). In India, 61% of all bamboo species can be found in areas with 1,500-4,000 mm rainfall per year (Biswas, 1988). Qiu *et al.* (1992) presented for *P. pubescens* in China a highly significant relationship ($y = 35 \cdot \log x - 90$) between annual precipitation (x, in mm) and annual timber yield (y, unit not specified). Kigomo and Kamiri (1985) found a similar functional dependency for *Oxytenanthera abyssinica* in Kenya. Many authors note the generally positive effects of greater availability of water on bamboo production and how lack of water limits its productivity. Lin (1995) said that irrigation promotes shoot and culm growth when rainfall is insufficient, Koyama and Uchimura (1995) pointed to the high water requirement for culm elongation, and Huang *et al*. (1993) showed that in locations with little available soil moisture, low biomass accumulation is largely partitioned below ground. It is known that wet summers increase shoot production of sympodial bamboo (Pearson *et al*., 1994), and that bamboo is not a suitable commercial species for areas where sufficient water is usually not available (Siddiqui, 1994). Only very few studies, however, have attempted to quantify water usage of bamboo. Kleinhenz and Midmore (2000) estimated the maximal annual water dissipation rate of bamboo to be about 3,300 mm rainfall equivalent. Midmore *et al*. (1998) stated that successful cultivation of *P. pubescens* in semiarid parts of Australia depends primarily on frequent but nonexcessive additions of water through precipitation and irrigation (>2,000 mm per year).

Not only general demand for high water availability but also availability of water during specific growth stages may affect bamboo productivity. The detrimental effects of drought but positive effects of irrigation during the shoot and culm growth phase were outlined by Chu and Xu (1988), Li and Zhang (1987), and Lin (1995). Fu and Banik (1995) stated that irrigation was required for intensively managed shoot stands after 10 days without rainfall during the shoot season. Midmore *et al*. (1998) stressed the need to pay attention to water

Table VI

Standing-Culm Density, and Yield of Different Products of Several Bamboo Species

Bamboo species	Product	Standing-culm density (culms/ha)	Annual yield (t/ha)	Comments	Reference
Monopodial species					
Acidosasa notata	shoots	9000-12000	9-11	—	Zheng *et al*. (1996a)
Bashania fargesii	timber	7400-11000	10-11	—	Tang and Wei (1984)
Phyllostachys fimbriligula	shoots	9600-10200	31	—	Cai and Wang (1985)
Phyllostachys makinoi	timber	4900	30	—	Hwang, 1975
Phyllostachys makinoi	shoots and timber	3000-4000	—[a]	richer site	Yang and Huang (1981)
Phyllostachys makinoi	shoots and timber	8000-14000	—[a]	poorer site	Yang and Huang (1981)
Phyllostachys nidularia	timber	52500	11	—	Zhang *et al*. (1997)
Phyllostachys nidularia	shoots or timber	50000	20 or 14	—	Shen *et al*. (1993)
Phyllostachys nidularia	shoots and timber	50000	—[a]	—	Hu *et al*. (1995)
Phyllostachys nigra	timber	15000	—[a]	—	Hu (1988)
Phyllostachys nigra	timber	22000-27000	—[a]	—	Zhang and He (1997)
Phyllostachys pubescens	shoots	1600	7-28	depending on soil quality	Oshima (1931b)
Phyllostachys pubescens	shoots	1700	7	temperate climate conditions	Hu and Pan (1983)
Phyllostachys pubescens	shoots	2200	10-20	—	Fu and Banik (1995)
Phyllostachys pubescens	shoots	1800-3300	—[a]	for big-sized shoots	Hu (1988)
Phyllostachys pubescens	shoots	3000-3700	—[a]	—	Yu (1988)
Phyllostachys pubescens	shoots	10500-12000	—[a]	for medium-sized shoots	Hu (1988)
Phyllostachys pubescens	shoots	9000-15000	—[a]	for small-sized shoots	Hu (1988)
Phyllostachys pubescens	shoots and timber	1800	—[a]	—	Hu and Pan (1983)
Phyllostachys pubescens	shoots and timber	2100	—[a]	—	Chen (1981)
Phyllostachys pubescens	shoots and timber	3000-4000	—[a]	—	Yang and Huang (1981)
Phyllostachys pubescens	shoots and timber	3000-4500	—[a]	—	Qiu *et al*. (1992)

Phyllostachys pubescens	timber	1500	<3.5	low production	Fu and Banik (1995)
Phyllostachys pubescens	timber	1500-2300	10	—	Fu *et al*. (1991a)
Phyllostachys pubescens	timber	2300	3.5-7.0	medium production	Fu and Banik (1995)
Phyllostachys pubescens	timber	3000	7-10	high production	Fu and Banik (1995)
Phyllostachys pubescens	timber	3200	9	—	Fang *et al*. (1997b)
Phyllostachys pubescens	timber	3300	24	—	Cheng (1983)
Phyllostachys pubescens	timber	4600	—[a]	—	Liao (1986)
Phyllostachys pubescens	timber	4000-8000	—[a]	—	Suzuki and Narita (1975)
Phyllostachys pubescens	pulp and paper	3000-4500	—[a]	—	Fu and Banik (1995)
P. viridis, P. glauca, P. bambusoides	shoots	9000-12000	10-20	depending on size of species	Fu and Banik (1995)
P. viridis, P. glauca, P. bambusoides	timber	10000-15000	—[a]	depending on size of species	Fu and Banik (1995)
P. vivax, P. glabra, P. praecox	shoots	12000-15000	—[a]	depending on size of species	Ma *et al*. (1988)
Sympodial species					
Bambusa glaucescens	shoots and timber	3000-3900	—[a]	—	Thanarak (1996)
Bambusa oldhamii	shoots	9600-18000	12-15	—	Lin (1995)
Dendrocalamus asper	shoots	3000-11000	—[a]	—	Kao and Chang (1989)
Dendrocalamus asper	shoots and timber	2200-3100	—[a]	—	Thanarak (1996)
Dendrocalamus latiflorus	shoots	900	13	—	Chen (1993)
Dendrocalamus latiflorus	shoots	7000-14000	10-30	—	Fu and Banik (1995)
Dendrocalamus strictus	timber	1700	0.7-2.0	—	Siddiqui (1994)
Dendrocalamus strictus	timber	1900	1	—	Prasad (1987)
Dendrocalamus strictus	timber	15000-21000	—[a]	on marginal land	Patil *et al*. (1994)
Dendrocalamus strictus	pulp and paper	6700-22200	—[a]	—	Fu and Banik (1995)
D. strictus, B. bambos, B. textilis	timber	7000-14000	3-10 (15-33)	depending on size of species	Fu and Banik (1995)
Oxytenanthera abyssinica	timber	43000	37	—	Kigomo and Kamiri (1985)
Thyrostachys siamensis	pulp and paper	4400-10400	—[a]	—	Kaitpraneet *et al*. (1981)

[a] No information provided

supply just before and during shoot production. Thanarak (1996), however, suggested that the harvest of *D. asper* could be brought forward by irrigating stands during the dry preshoot season, whereas Wan (1994) emphasized the need for irrigation during rhizome growth to ensure survival of new culms. Given that temperatures are sufficiently high for sympodial bamboo growth, bamboo could produce new shoots and culms year-round, with no distinct shoot phase if water demand is satisfied by rainfall (Farrelly, 1984) or irrigation. Therefore, when there are no restrictions on water supply, productivity of sympodial bamboo may be maximized with year-round irrigation. Such is evident with a similarly managed species, asparagus. The benefits of constant warm temperatures and water supply are exploited for year-round cultivation of asparagus in several sub-/tropical regions including Thailand (Jayamangkala, 1992), Ecuador (Krarup, 1996) and Chile (Delgado de la Flor and Oordt, 1996). If water supply is limited, irrigation before, during, and after the shoot phase will have greater impact on production increase. While growth of monopodial species is constrained by low temperature in winter, it is unlikely to respond markedly to supplementary irrigation at this time. In subtropical regions, however, increased water availability early in spring can bring forward the growth and appearance of new shoots (Midmore *et al.*, 1998).

B. Soil Physical Properties

Due to the immense diversity of soils and complexity of interactions between soil parameters, it is difficult to relate bamboo growth across sites to specific soil factors. Bamboo is known to grow in "poor" soils (Sutiyono, 1987) and is therefore used for rehabilitation of degraded land (Desh, 1990; Rao *et al.*, 1999). In natural bamboo forests and in stands under low-input conditions, the nutrient-supplying capacity of soils is usually the most important soil property governing bamboo growth and yield (Section III.C; Chen *et al.*, 1996). Soil physical factors, such as slope of land, texture, bulk density, moisture-holding capacity, and temperature, however, are among the nonchemical properties of soil which influence bamboo productivity.

New rhizomes in monopodial bamboo species are located at diminishing soil depths since they are produced from axillary buds on the top of older rhizomes. As the stand ages, rhizomes of older plants may become exposed to the soil surface (Oshima, 1931a). Except under very intensive bamboo cultivation, this does not seem to seriously affect productivity. The fact that monopodial bamboo species such as *P. pubescens* cover vast areas of partially steeply sloping land in China, and are recommended for soil conservation and erosion control on slope land (Storey, n. d.; Storey, 2000) may substantiate this. In contrast, the pachymorph rhizome of sympodial species is confined to much less soil volume (Farrelly, 1984) and is, therefore, more subject to erosion. Since the culm base of new shoots is always positioned higher than the culm base of shoots of the previous generation, rhizome and roots arise from progressively higher levels and are eventually exposed (Farrelly, 1984; Lin, 1995). Exposure of rhizome buds to sunlight prevents their development into shoots (Chaturvedi, 1988). Therefore, it is not surprising that natural stands of clumping bamboo species are more likely to be found on flat land where they prosper and grow better (Hassan *et al.*, 1988; Fu and Banik, 1995). Virtucio *et al.* (1994) studied the performance of planted stands of *Sphaerobambos philippinensis* on hill- and flatland in the Philippines. Although soil quality was better on the flatland site, standing-culm density and culm yield (2,400 culms/ha and 4.8 t dry weight/ha) on the hill-land site were much lower than on the flatland site (4,400 culms/ha and 18.5 t dry weight/ha). They concluded that this clumping bamboo species has a greater and potentially more sustainable yield potential on flat land. Annual additions of soil or mulch to individual clumps is a countermeasure to prevent exposure of rhizomes but is laborious and prone to erosion on steep slopes. Therefore, out of preference clumping bamboo species should not be planted on sloping land. If they must be planted on sloping land, they should be planted on terraces to overcome their propensity to soil erosion. In line with sympodial bamboo, monopodial bamboos appear to be more productive on flatland: in Taiwan, planting density of such bamboo is lower on sloping land than on flat land since sloping land cannot support high plant densities (Tai, 1985; Leong *et al.*, 1991). Likewise, He and Ye (1987) found negative relationships between increasing slope and culm yield in six locations in China. Zhang *et al.* (1996) showed that with *P. nidularia* yields decreased with increasing slope from 10.6 t/ha at <10° slope to 7.0 t/ha between 10 and 30° slope, and 3.6 t/ha at >30°.

Among soils of many bamboo-growing sites in China and Korea, soil texture was one of the most important parameters explaining variations in yield of *P. pubescens*. Culm yield of *P. pubescens* was negatively correlated with the percentage of <0.1 mm soil particles (He and Ye, 1987) and clay content (Hong, 1994). Bamboo growth parameters (i.e., culm height and diameter) were negatively related to sand and clay content but positively related to silt content in Korea (Chung and Ramm, 1990). This indicates that soils, which are rich in small soil particles such as heavy clay soils, are less suitable for bamboo production. This can be explained by their effect on growth of underground plant parts of bamboo: soils rich in smaller-size soil particles have greater bulk density which restricts rhizome (and root) growth (Wu, 1984). Xie and Ye (1997) reported results on the introduction of bamboo (*P. praecox*) to paddy rice fields. Due to unfavorable soil physical properties characteristic of this environment, growth of nonaquatic crops under nonflooded conditions is constrained (Kleinhenz, 1997). Although Xie and Ye (1997) did not record yields, they successfully established bamboo under such adverse conditions, stressing the need for soil improvement measures to relieve drought and prevent waterlogging. Soils too light in texture are also not suitable for bamboo growth either, but for different reasons. Jin and Wang (1997) were able to establish *B. oldhamii* on a seashore in China, but the water-holding capacity of such light soils was too low to satisfy the great demand of bamboos for water unless irrigation was applied.

Important management techniques employed to improve soil physical conditions in bamboo stands are tillage, use of covers and mulches, and culm management. Ling (1984), Wu (1984), Wan (1994), and Lin (1995) recommend tillage during the nonshoot season to improve soil physical properties for better growth of shoots, rhizomes, and roots through the soil. This is in contrast to studies by Xia *et al.* (1993) who recorded poorer bamboo yields with tillage, possibly as a consequence of damages to the root system (Christanty *et al.*, 1997). Oshima (1931a) stated that cultivation deeper than 50 cm for extension of roots to that depth is "useless." Lin (1995) and Fu *et al.* (1991a) recommend a maximum soil depth of 6-25 cm for both monopodial and sympodial bamboo species although Yu (1991) noted an improvement in yield in an established stand of *P. pubescens* after deep plowing for 3-4 years. Possible schedules for tillage (Fig. 1a) are: before the shoot season (Fu and Banik, 1995; Lin, 1995), after the shoot season/before rhizome growth (Nonaka, 1989; Wan, 1994), and before maximum root growth (Wan, 1994). To alleviate alternation in monopodial bamboos, several authors (e.g., Zheng *et al*., 1996a) recommend restricting tillage to the "off year."

The main purpose of using covers and mulches in bamboo stands is to protect rhizomes, roots, and new shoots from excessively warm or cold temperatures and from solar radiation (Oshima, 1931b; Ling, 1984; Cai and Wang, 1985; Chaturvedi, 1988; Fu and Banik, 1995; Zheng *et al*., 1996a; Zheng *et al*., 1996b). To avoid loss in quality of fresh edible bamboo shoots, e.g., by greening, early aging, and deterioration in taste, Lin (1995) and Thanarak (1996) recommend covering the growing area with soil, mulch, and/or plastic materials. Under tropical conditions, mulches can protect against excessive temperature and intense solar radiation (Oshima, 1931b). Bamboos planted under partial shade of trees or agricultural crops (e.g., banana and papaya) may derive benefit from their windbreak, and weed control properties (Siddiqui, 1994; Thanarak, 1996).

In contrast, mulches are maintained in temperate bamboo forests especially to insulate the soil against heat loss, thereby boosting physiological activity of bamboo plants, stimulating early and prolonged shoot development, and improving total yields (Suzuki and Narita, 1975; Wan, 1994; Cao *et al*., 1995a; Cao *et al*., 1995b; Feng *et al*., 1996; Shen *et al*., 1996; Fang *et al*., 1997a; He *et al*., 1997). Jin *et al*. (1998), however, concluded that mulching can significantly reduce bud formation on rhizomes. Whether under tropical or temperate conditions, natural covers and particularly bamboo leaves (Joshi *et al*., 1991) are preferable to artificial covers such as cover-cloths (Chang and Junag, 1985). Their decomposition by microorganisms provides extra heat energy that promotes early shoot growth in temperate climates. Mulches conserve soil moisture by reducing evaporation (Thanarak, 1996) and enhance other soil properties including reduction in bulk density, improved water-holding capacity, improved cation exchange capacity, weed control, erosion control, reduced surface water run-off, and maintenance of soil organic matter.

Christanty *et al*. (1997) describe the development of a profuse system of fine and small roots by bamboo within the mulch layer and the mineral soil surface providing for efficient nutrient absorption. This may explain why mulching in combination with fertilizer application significantly improved yields of *P. pubescens* (Lü and Liu, 1984). A special form of mulch is "living mulch," i.e., green manure plants (usually N-fixing legumes) grown in between bamboo plants. Oshima (1931a) suggested maintaining a grass mulch which is repeatedly mowed in *P. pubescens* stands and Patil *et al*. (1994) stated that *Sesbania grandiflora* produced a "high mulch biomass" in *D. strictus* without negatively affecting bamboo growth. Living-mulch, however, was found to compete with bamboo for growth resources such as water and nutrients when introduced to low standing-culm density bamboo stands with high rates of transmission of solar radiation below the bamboo canopy (Hong, 1994). While Mao and Bin (1998) suggest intercropping bamboo with leguminous crops only during the first year after planting, others such as Fu and Banik (1995) recommend that living mulch should not be introduced earlier than 1-3 years after establishing a bamboo stand.

Greater standing-culm density results in greater leaf area per unit soil surface area (i.e., leaf area index), preventing light penetration to the soil surface. Under tropical conditions, this may favor absorption of photon-flux density, maximize canopy photosynthesis, and prevent excessive heating of the soil. For earlier edible shoot harvest in temperate climates, however, lower standing-culm densities in bamboo stands are preferred since their sparse canopies allow more solar radiation to penetrate to the ground and warm the soil (Hu and Pan, 1983). In practice, the desired balance between loss of yield potential and price premiums for earlier harvests will dictate the chosen standing-culm density in temperate climates. Another innovative practice to stimulate earlier shoot growth is to increase temperature of rhizomes by directly exposing them to sunlight during early spring (Oshima, 1931b; Fu and Banik, 1995; Lin, 1995). Once the soil covering rhizomes is removed for 1-2 weeks, exposed rhizomes are buried again.

C. SOIL CHEMICAL PROPERTIES

Nutrient availability is the most important soil chemical property governing bamboo growth and yield but other factors such as soil pH and soil salinity are also important. The contents of available nutrients in the soil are positively related to yield and explain much of the variation in yield across bamboo-growing sites and regions in China (He and Ye, 1987; Hong, 1994). Hence, bamboo growth and biomass is positively related to soil organic matter, which is a primary source of nutrients in bamboo cultivation sites in Korea (Jin and Chong, 1982; Chung and Ramm, 1990). Nutrient availability depends not only on the inherent fertility of a soil, but also on whether bamboo stands are harvested, cultivated, and/or nutrients are applied externally.

1. "Native" Soil Chemical Properties

Soil pH and salinity are factors which affect bamboo in both natural stands and cultivated plantations. There is a positive trend towards better growth of bamboo under higher soil pH (Jin and Chong, 1982; Chung and Ramm, 1990). Cai and Wang (1985), however, measured best growth of *P. fimbriligula* at a soil pH of about 5.2 and suboptimal growth below and above this value. This implies that, in contrast to other crops, bamboos are comparably less affected by acid soils, making them suitable for cultivation on degraded land in sub-/tropical regions where soils are frequently highly weathered and, therefore, low in pH. Most bamboo species do not tolerate saline soil conditions. Productivity of *P. vivax* in a coastal area, however, was acceptable (Sun *et al*., 1996) and Jin and Wang (1997) were able to achieve good productivity of *B. oldhamii* on a seashore of China although the salt content (>0.4%) in soil did impact negatively on growth.

Litter biomass contributes significantly to soil organic matter and supplies bamboos with nutrients in natural stands and cultivated plantations (Section II.D). Nutrient supply from litter is delayed and sustained since the biomass must first be decomposed (Cao *et al*., 1997; Kleinhenz *et al*., 1997a). Decomposition of litter and mineralization of nutrients from litter depend on environmental conditions (Cao and Luo, 1996). Not surprisingly, Fu *et al*. (1989) conclude that constant warm temperatures and sufficient moisture and humidity promote activity of microbial decay organisms, their decomposition of litter, and release of nutrients. Litter may be categorized into three fractions (Christanty *et al*., 1996): (1) intact fraction, (2) fragmented fraction, and (3) decomposed fraction. Within the first year after litter fall, the litter biomass is still intact, after 3 years it is partly decomposed, and after 4 years, fractions of litter biomass were composed of intact, fragmented, and decomposed material. Decomposition in temperate climates is slow with 6 years required for 95%

decomposition (Fu *et al*., 1989), whereas in tropical climates, more than 50% of litter biomass decomposes within 1 year (Tripathi and Singh, 1992). It follows that the litter biomass in a temperate bamboo stand will increase for up to 6 years until equilibrium is reached between additions of litter biomass and their complete decomposition. Therefore, bamboo litter acts as a slow-release reservoir for nutrients and should ideally not be removed or used for other purposes (e.g., as animal fodder).

Harvesting and cultivation of bamboo stands remove biomass and cause soil disturbance. The organic root material is transformed into soil organic matter but soil aeration subsequently promotes growth of aerobic soil microorganisms which decompose soil organic matter. This initially ties up, i.e., immobilizes, nutrients during buildup of microbial tissue. The fraction of nutrients in microbial form, however, is extremely labile and as microbial populations decrease, these nutrients are rapidly mineralized. Soil chemical properties in unharvested and harvested bamboo stands were compared by Raghubanshi (1994). He measured a decrease in total N but increases in fractions of microbial and mineralized N in the harvested stand compared with the unharvested stand. Some authors recommend soil cultivation to increase availability of nutrients (e.g., Nonaka, 1989; Lin, 1995). Aeration of soil promotes mineralization of nutrients but Christanty *et al*. (1997) showed that hoeing in an Indonesian bamboo forest killed approximately 19 t/ha of fine and small roots which, although it improved soil organic matter and presumably availability of nutrients, reduced bamboo vigor considerably. When harvesting and cultivation of bamboo stands continue for longer periods and removed nutrients are not replenished, the nutrient-supplying capacity of soils will decrease (Lou *et al*., 1997).

2. Nutrient Management

In contrast to other soil physical and chemical properties, nutrient availability can be managed comparably easily through fertilization. It is generally agreed that fertilization can have dramatic impacts on bamboo productivity under “poor” site conditions and under minimal management. Oshima (1931a) said that as with vegetable cultivation, bamboo requires abundant fertilizer, but no studies show that excessive fertilizer application reduced its yield and quality. Hong (1987) recognized the particularly beneficial effect of fertilizer application on bamboo production on poor soils in China. Ahmad and Haron (1994) recommended regular fertilization for optimum bamboo growth and performance in Malaysia. Widjaja (1991) described fertilization as the most important management technique in Indonesia. Meanwhile, Qiu *et al*. (1992) concluded that productivity of bamboo forests under minimum management in China could be significantly increased by fertilizer application. Fertilizers dramatically increased bamboo yield in India (Lakshmana, 1994a) and in Japan (Suzuki and Narita, 1975). As for many other agricultural and horticultural crops, nutrient application rates, ratios between nutrients, schedules of nutrient application, form of fertilizer, and nutrient placement are equally important considerations in bamboo production. Since bamboo is a perennial crop, however, nutrient management schemes that have been developed for annual crops may not apply to it. Moreover, bamboo is grown for several products, and it is understandable that optimal fertilization will vary with purpose of cultivation. Due to increasing scarcity of resources in the future, there is a need to match efficient fertilizer use to sustained productivity, and to sustain favorable soil conditions over the short and long term.

a. Nutrient Application Rates and Nutrient Ratios

Due to their absolute lower nutrient-absorption capacity, seedlings and young plants require less nutrients than mature plants. Shanmughavel and Francis (1997), Raina *et al*. (1988), Thanarak (1996), and Totey *et al*. (1989) have recommended nutrient application rates for seedlings and young plants of *B. bambos*, *B. tulda*, *D. asper,* and *D. strictus*, respectively. More importantly, Table VIII presents an overview of reported annual nutrient application rates for, and ratios between, N, P, and K for mature bamboo stands. Nutrient applications average 318, 149, and 126 kg/ha/year N, P, and K (N:P:K ratio: 2.5:1.2:1.0). Many more nutrients are applied in stands primarily used for edible shoots (523, 226, and 228 kg/ha N, P, and K) than in stands for shoot and timber production (315, 97, and 142 kg/ha N, P, and K) and timber-only stands (225, 135, and 89 kg/ha N, P and K). Compared with the average nutrient content of total plant biomass, which is 288, 44, and 324 kg/ha of N, P, and K with an N:P:K ratio of 7:1:7 (Section II.D), application rates appear excessive since only a proportion of that total biomass is harvested annually. For example, nutrients removed in fresh shoots (on average 16 t/ha/year yield; 5-10% dry weight; 4.0, 0.6, and 4.0% N, P, and K) average at 49, 7, and 49 kg N, P, and K/ha/year and those in culms for timber (on average 13 t/ha/year yield; 50% dry weight; 0.6, 0.1, and 1.0% N, P, and K) at 36, 9, and 63 kg N, P, and K/ha/year (Tables IV, V, and VII; Kleinhenz and Midmore, unpublished data). At its maximum, about 85, 16, and 112 kg N, P and K/ha/year are removed when bamboo is grown for shoot and timber which is approximately 30, 37, and 35% of the total content of N, P, and K of a bamboo stand. In perennial crops such as bamboo, however, calculation of fertilizer rates cannot be based upon balancing nutrient removal through harvest with nutrient application, as is done in annual crop production. A great part of nutrients added promotes stand biomass that is not harvested, i.e., roots, rhizomes, and standing culms, indirectly improving yield. This is so for the period before bamboos reach maximum stature and productivity. As such, Toky and Ramakrishnan (1982) showed that *D. hamiltonii* accumulated soil potassium only for a few years after clear felling. This suggests that addition of nutrients in excess of those removed through harvest is favorable during earlier growth stages but may not be required once plants reach their maximum stature. At that growth stage, application rates should preferably be oriented towards the amount of nutrients removed through harvest with some allowance for leaching and fixation.

Data for average fertilizer-use efficiency of applied N, P, and K follow the same pattern as average nutrient content of plants: K>N>P (Table IX). This and the recognized low rates of K application indicate that application of potassium is the most important measure to improve bamboo productivity. Toky and Ramakrishnan (1982), Rao and Ramakrishnan (1989), Tewari *et al*. (1994), and Shanmughavel and Francis (1997) pointed to the importance of potassium for growth of bamboo. In general, K application rates appear to be too low and because of the high K-use efficiency, increased rates could result in a significant increase in productivity, particularly in timber production. In contrast, general application rates for P appear to be too high and an increase of P rate is unlikely to increase productivity. Current N application rates for the different purposes for which bamboo is grown would appear to be more realistic.

Table VII

Age Structure of Standing Culms [(% of Total Number of Standing Culms) or (Culms/Plant)], Felling Age of Culms and Harvested Yield of Several Bamboo Species Cultivated for Different Products

		Culm age (years)								Felling age	Yield	
Bamboo species	Product	1	2	3	4	5	6	7	8	(year)	(t/ha/year)	Reference
Monopodial species												
Acidosasa notata	shoots	25%	25%	25%	25%					5	7	Zheng *et al*. (1996a)
Phyllostachys fimbriligula	shoots	25%	25%	25%	25%					5	—[a]	Cai and Wang (1985)
Phyllostachys makinoi	timber	50%	50%							—	16	Hwang, 1975
Phyllostachys praecox	shoots	33%	33%	33%						4	—	Liu and Pan (1994)
Phyllostachys pubescens	shoots	33%		50%		10%		7%		—	8	He and He (1983)
Phyllostachys pubescens	shoots	33%		33%		33%				6-8	7-28	Oshima (1931b)
Phyllostachys pubescens	shoots	38%	38%	24%						4	—	Wan (1994)
Phyllostachys pubescens	shoots or timber	33%		33%		33%		1%		7	10-20; 4-10	Fu and Banik (1995)
Phyllostachys pubescens	shoots and timber	20%	20%	20%	20%	20%				6	—	Chen (1981)
Phyllostachys pubescens	shoots and timber	22%	33%	39%	6%					—	2 and 15	Zheng *et al*. (1996a)
Phyllostachys pubescens	shoots and timber	25%		25%		25%		25%		>8	—	Qiu *et al*. (1992)
Phyllostachys pubescens	shoots and timber	1-15								—	—	Suzuki and Narita (1975)
Phyllostachys pubescens	timber	50%		50%						4-5	—	Oshima (1931b)
Phyllostachys pubescens	timber	—	8%	67%	21%					5	13	Huang, (1984)
Phyllostachys pubescens	pulp and paper	30%	27%	43%						—	31	Ma *et al*. (1996)
P. viridis, P. glauca, P. bambusoides	shoots or timber	33%	33%	33%	1%					4	10-20	Fu and Banik (1995)
Sympodial species												
(in general)	shoots	3-4	3-4							3	—	Fu and Banik (1995)
(in general)	shoots and timber	2-3	2-3	2-3						4	—	Farrelly (1984)
Bambusa bambos	timber	5		4		1				—	—	Shanmughavel *et al*. (1997)
Bambusa oldhamii	shoots	4-6	4-6	4-6						—	12-15	Lin (1995)
Bambusa oldhamii	shoots	—	5	1						—	6	Chang and Junag (1985)
Bambusa prevariabilis	shoots and timber	3	3	3						4	3 and 9	Fu and Banik (1995)
Dendrocalamus asper	shoots and timber	4-5	4-5	4-5						4	—	Thanarak (1996)
Dendrocalamus asper	shoots and timber	2	2	2	2					5	—	Kao and Chang (1989)
Dendrocalamus latiflorus	shoots	3-4	3-4	2-3						4	—	Fu and Banik (1995)
Dendrocalamus latiflorus	shoots	—	5	1						—	9	Chang and Junag (1985)
Dendrocalamus strictus	timber	10	11							—	—	Prasad (1987)
Schizostachyum lumampao	timber	11	11							—	7	Virtucio and Tomboc (1994)

[a] No information provided

Table VIII

Annual Application Rates of Nutrients (N, P and K), N:P:K Ratios and Harvested Yield of Several Bamboo Species Cultivated for Different Products

Bamboo species	Product	Nutrient application rate (kg/ha/year) N	P	K	N:P:K ratio N	P	K	Yield (t/ha/year)	Reference
(in general)	shoots or timber	≈225-570 each			4-5	3	1	10-30	Fu and Banik (1995)
(in general)	shoots or timber	110	110	110	1	1	1	—[a]	Farrelly (1984)
Monopodial species									
Phyllostachys nidularia	timber	87	78	8	2.5	1.0	1.5	19.3	An *et al*. (1995)
Phyllostachys nidularia	timber	373	80	100	4.7	1.0	1.3	—	Shen *et al*. (1993)
Phyllostachys praecox	shoots	750	167	333	4.5	1.0	2.0	4.5-6	Liu and Pan (1994)
Phyllostachys pubescens	shoots	98	—	—	—	—	—	7.9	Jeong *et al*. (1995)
Phyllostachys pubescens	shoots	300	300	300	1	1	1	30	Fu *et al*. (1991a)
Phyllostachys pubescens	shoots	≈882	—	—	—	—	—	8.2	Yu (1987)
Phyllostachys pubescens	shoots and timber	276	110	166	2.5	1	1.5	4.0 and 7.6	Wang *et al*. (1996)
Phyllostachys pubescens	shoots and timber	310	83	118	3.7	1.0	1.4	1.4 and 15	Hong (1994)
Phyllostachys pubescens	timber	131	—	—	—	—	—	12.4	Shi and Bian (1987)
Phyllostachys pubescens	timber	183	66	40	4.6	1.7	1.0	6.9	Xiang and Xi (1987)
Phyllostachys pubescens	timber	200	120	140	1.7	1.0	1.2	—	Suzuki and Narita (1975)
Phyllostachys pubescens	timber (site 1)	214	286	214	1.0	1.3	1.0	16.4	Hong (1987)
Phyllostachys pubescens	timber (site 2)	214	429	71	3	6	1	33.6	Hong (1987)
Phyllostachys pubescens	timber	276-414	—	—	—	—	—	25	Huang and Wang (1996)
Phyllostachys pubescens	timber	≈400	—	—	2	1	1.5	25	Lü and Liu (1994)
Phyllostachys pubescens	timber	460	—	—	—	—	—	4.1	Wang (1988)
Phyllostachys propinqua	shoots	760	210	50	15	4	1	≈20	Shen *et al*. (1996)
Phyllostachys reticulata	timber	—	—	—	3.4	1.0	2.3	—	Jin and Chong (1982)
Sympodial species									
Bambusa distegia	timber	70	10	79	40	1	49	—	Zhou and Wu (1997)
Bambusa oldhamii	shoots	≈345	—	—	—	—	—	12-15	Lin (1995)
Dendrocalamus asper	shoots and timber	≈370-440	—	—	1	1	1	—	Thanarak (1996)
Dendrocalamus strictus	timber	45	45	45	1	1	1	—	Lakshmana (1994a)
Dendrocalamus strictus	timber	200	100	100	2	1	1	—	Patil *et al*. (1994)
Thyrostachys siamensis	shoots and timber	270	—	—	—	—	—	—	Thanarak (1996)

[a] No information provided

Table IX

Average Fertilizer-Use Efficiency[a] of N, P and K in Bamboo Production for Shoots and Timber

	Fertiliser-use efficiency (t yield / kg nutrient)		
	Bamboo product		
Nutrient	Shoots	Timber	Average
N	0.03	0.17	0.13
P	0.04	0.02	0.02
K	0.08	0.54	0.45

Note. [a] Calculated from published data
Data source: An *et al*. (1995), Fu *et al*. (1991a), Hong (1987), Hong (1994), Huang and Wang (1996), Jin and Chong (1982), Wang (1988), Wang *et al*. (1996), Xiang and Xi (1987)

Nutrient management must not only satisfy requirements for yield but also for quality of harvested parts. Very little research has been conducted on the effects of fertilizer application on the many quality parameters of fresh edible shoots and bamboo timber. There is, however, a general trend that with more N, P, and K applied, total yields of shoots and/or timber are higher due to the greater number of shoots and/or culms harvested, and longer culms, but, their diameter is reduced (Hong and Jiang, 1986; Hong, 1994). Tissues of shoots and culms harvested from plantations abundantly supplied with nutrients, however, are usually “softer,” resulting in lower shoot quality and less durable culms with poorer mechanical properties (Ueda, 1960). For edible shoots, higher N decreases but higher P increases sugar content in *P. pubescens* (Hong, 1994). For the same species, Zhu *et al*. (1991) quantified the effects of N, P, and K on shoot quality with the following results:

- N, P, or K enhance amino acid content
- N decreases sugar content
- P increases sugar content
- N increases hydrolytic acids
- N and/or P lower free tyrosine of canned shoots

Silicon has a special role in the nutrition of bamboo, because it is associated with cell wall constituents and is present in xylem cell walls and fibers of plants. There is a general agreement that Si should only be applied to bamboo stands for timber production. For production of edible shoots, Si may prevent shoot development and reduce quality by increasing fiber content (Hamada, 1982; Hong, 1994; Fu and Banik, 1995). In contrast, application of Si improves the mechanical properties of bamboo culms with about 16 kg Si removed in 1 t of timber (Nonaka, 1989). Recommendations for Si application to bamboo timber stands range from 0.2 (Xiang and Xi, 1987) to 6 (Farrelly, 1984) and 16 (Lü and Liu, 1984; Nonaka, 1989) kg SiO_2/ha/year.

b. Scheduling of Nutrient Application

As for many other crops, bamboo responds more favorably to split application of nutrients throughout the year than to a single annual dressing (Raina *et al*., 1988). Whether nutrients are applied as single or multiple dressings, the optimum time of application during the year is of particular interest. These usually coincide with distinct growth phases in bamboo:

- before the shoot season
- during the shoot season
- after the shoot season/before rhizome growth
- during rhizome growth
  - during bud formation on rhizomes
  - during shoot growth below-ground

Several studies have systematically tested the benefits of nutrient application during different times of the year on bamboo productivity; however, no single, most important stage was identified. Nutrient application earlier in the season, i.e., shortly before and during the shoot season, may be the most appropriate time of fertilizer application (Shen *et al*., 1993; Jeong *et al*., 1995). Hong (1994) concluded that nutrient demand of bamboo is greatest during periods of rapid growth, i.e., of shoots and rhizomes. Therefore, a second dressing during rhizome growth and/or when buds on rhizomes start developing into new shoots was found to be favorable (Hong, 1994; Wang *et al*., 1996). These recommendations were developed for cultivation of monopodial bamboo in temperate regions. These regions are usually characterized by the occurrence of some rainfall during the nonshoot season, which improves availability of nutrients to plants. Under sub-/tropical conditions, this preshoot season is typically dry and application of fertilizer may be ineffective without irrigation. Mohamed (1995) concluded from his experiments in tropical Malaysia that no nutrient was released from fertilizer granules in the absence of water during the dry season. If mineralized nutrients accumulate in the soil during the dry season, fertilizer application would be unnecessary because negligible leaching of mineralized nutrients would take place (Kleinhenz *et al*., 1997b). In support of this, Raghubanshi (1994) showed that highest concentrations of available nutrients and of microbial biomass in a bamboo savannah in India were found during the dry season. Table X presents an overview of reported schedules of nutrient application to bamboo. Most authors recommend multiple dressings with at least one focused shortly (1 month) before aboveground emergence of shoots. This dressing may be N based whereas applications later in the growing season, i.e., during rhizome growth, may be P and K based. For silicon, Huang (1987) recommended splitting applications throughout the growing season.

Special production requirements dictate that these general schedules be modified. For example, for production of "early" shoots after the winter or dry season, several authors recommend an additional N dressing. Thanarak (1996), Fang *et al*. (1997a), and Li *et al*. (1998c) recommended applying up to 460 kg N/ha and achieved earlier shoot emergence by up to 20 days for *D. asper*, *P. praecox,* and *P. pubescens*, respectively. To contend with alternation in monopodial bamboo species a long-term biennial fertilization schedule was recommended (Anonymous 1986) with nutrients applied only in the "off season" to improve the photosynthetic capacity of the (low) total leaf area of plants (Section II.B).

Table X

Schedules of Fertilizer Application and Fertilizer Form in Bamboo Species Cultivated for Different Products

		Schedule / growth phase					
					During rhizome growth		
Bamboo species	Product	Before shooting	During shooting	Before rhizome growth	During bud development	During below-ground shoot growth	Reference
(in general)	—[a]	inorganic	—	inorganic	organic		Fu and Banik (1995)
(in general)	—	1 month before	—	×[b]	—	—	Farrelly (1984)
Bambusa oldhamii	—	organic	inorganic	—	—	—	Lin (1995)
Dendrocalamus asper	shoots and timber	organic and inorganic	inorganic	—	—	—	Thanarak (1996)
Gigantochloa scortechinii	timber	—	—	—	not during this season		Mohamed (1995)
Phyllostachys sp.	shoots	13 % inorganic N-based	—	32 % NPK	13 % NPK	42 % organic	Wan (1994)
P. nidularia	timber	×	—	—	×[c]		Shen *et al*. (1993)
P. propinqua	timber	×	—	×	×	×	Shen *et al*. (1996)
P. pubescens	shoots	×	—	—	×[c]		Fu *et al*. (1991a)
P. pubescens	shoots	×	—	—	—	—	Jeong *et al*. (1995)
P. pubescens	shoots and timber	—	×	—	×[c]		Hong (1994)
P. pubescens	shoots and timber	inorganic	—	—	organic / slow-release inorganic		Oshima (1931b)
P. pubescens	shoots and timber	—	—	—	×[c]		Wang *et al*. (1996)
P. pubescens	timber	N-based	inorg. N	—	P and K		Huang (1987)
P. pubescens	timber	1 month before	—	—	—	—	Fu *et al*. (1991b)
P. pubescens	timber	—	×	—	—	—	Fu *et al*. (1994)

[a] No information provided, [b] non-quantified application, [c] only specified as during rhizome growth

c. Fertilizer Form

There is no consensus on the preferable fertilizer form, i.e., inorganic or organic form, or on their short- and long-term effects on bamboo productivity and site (i.e., soil) quality. Effects very similar to those that accompany disturbance of bamboo soils through harvest and cultivation appear to accompany continuous (exclusive) use of inorganic fertilizers. This leads to less total N and soil organic matter but pools of readily available inorganic nutrients are greater (Jin and Chong, 1982). Organic fertilizers are slowly decomposed by microorganisms and, therefore, improve organic matter content of bamboo soils. Although response in bamboo plants is slower immediately after application, organic fertilizers exert a longer-lasting effect on "fertility" of bamboo soils than inorganic fertilizers (Wang *et al*., 1985). For intensive production of shoots and timber, a combination of organic and inorganic fertilizers, integrated with other crop management practices, may be the optimum solution. Liu and Pan (1994) reported that through such intensive management, including high application rates of inorganic fertilizers (e.g., 750 kg/ha N), of a *P. praecox* forest in China, output was 14.7 times that of the control. As a general practice, for quick response in bamboo, inorganic N-based fertilizers are preferable before and during the shoot season, whereas organic fertilizers are preferably applied during later growth stages (Table X).

d. Fertilizer Placement

Distribution of minerals takes place through the rhizome system of monopodial bamboo species (Qiu *et al*., 1986). Translocation to young, growing plant parts, however, decreases with distance from nutrient sources. Therefore, fertilizers should be placed close to younger plant parts, i.e., broadcast around young (≤1-year old) rhizomes (without aboveground culms), rather than applied as a spot dressing to older (>1-year-old) rhizomes (with aboveground culms). Similarly, Oshima (1931b) recommended applying fertilizers to younger rhizome parts before the shoot season when a quick response is required and to older rhizome parts when a slow but sustained effect is sought. The effects of fertilizer placement hold only for young bamboo stands since differences in bamboo productivity between broadcast and spot dressings diminish with stand age (Shi and Bian, 1987; Hong, 1994), probably because of the increasing density of the rhizome system. For sympodial bamboo, Lin (1995) recommended applying fertilizers as spot dressings around clumps for immediate effects before the shoot season and broadcasting fertilizers away from clumps for longer-term effects after the shoot season.

e. Fertilization Based on Plant Analysis

Determination of fertilizer application rates based on analysis of nutrient concentrations in plant parts is increasingly common in many crops including plantation/tree crops for production of fruits, nuts, and teak. The approach of Diagnosis Recommendation Integrated System (DRIS) is based upon establishing diagnostic norms for nutrients in specific plant parts and how they can be modified by fertilization. Together with other crop management practices, Ma and Zhang (1997) recommended such a system for intensive multipurpose cultivation of bamboo. The photosynthetic capacity of leaves largely depends on their chlorophyll content which, in turn, is positively correlated with the concentration of N in their tissues (Section II.B). There is no question that fertilizer application increases nutrient concentration in leaves of bamboo (Zhou and Wu, 1997; Li *et al*., 1998c). Shi and Bian (1987) showed specifically that N increases chlorophyll a, chlorophyll b, and consequently, total chlorophyll in *P. pubescens*. Therefore, monitoring and maintaining certain concentrations of nutrients such as N in leaves may be an alternative to fertilization schemes based upon fixed fertilizer rates and application schedules. In studies with *B. distegia*, Zhou and Wu (1997) found that nutrient concentrations in1-year-old leaves were better correlated with timber yield than those in <1-year-old leaves because the former were more responsive to soil nutrient concentration. Therefore, they concluded that 1-year-old leaves are suitable test tissues. However, there are no published diagnostic criteria for nutrient levels in bamboo. Midmore and Kleinhenz (2000) found a hyperbolic relationship between N application rate and leaf N concentration in *P. pubescens* and *B. oldhamii,* and showed that the relationship will vary with species and stand age. The authors suggested that a “lower limit” for leaf N may be 2.0%, the “optimum” about 3.0%, and the “upper limit” 3.5%.

IV. SUMMARY

Bamboo is an exceptionally diverse species group, covering vast land tracts especially in South, East, and Southeast Asia. Its range of uses for humans is extensive, and important among these are its use as fresh, edible vegetable shoots, and culms for timber. These uses are exploited at differing levels of intensity, ranging from gathering in the wild to intensive industrial exploitation for a multibillion-dollar industry worldwide. From an environmental perspective, bamboo fulfils many ecological functions, particularly, soil conservation and carbon sequestering. As for many other crops, demand for bamboo products is beginning to outstrip supply, resulting in overexploitation and exhaustion of bamboo resources. One of the major goals for the future is to increase productivity and resource use through improved management of growth and the growth environment.

Bamboos are categorized into monopodial (running) and sympodial (clumping and generally tropical) types according to the morphology of their (leptomorph and pachymorph) rhizomes. Despite this morphological difference, there is little difference in accumulation and partitioning of biomass between these two groups. Of the about 145 t/ha total biomass, 31-43% is partitioned into belowground plant parts. All bamboos develop exceptionally profuse and highly efficient root systems within a shallow soil layer, primarily to the 40-cm soil depth. This explains their rapid uptake of water and nutrients. Mature plants may be able to absorb as much as 3,300 mm of rainfall-equivalent water per year (33 million l/ha/year) and contain on average 288, 44, and 324 kg of N, P, and K per hectare.

In contrast to many other crops, bamboo is subject to an integral system of growth phases throughout the year that also depends upon the age structure of plant parts. Generally, growth of new leaves and culms commences after the winter or dry season followed by growth of new rhizomes and subsequently new roots. One basic difference between monopodial and sympodial bamboo is the growth cycle of their leaves: monopodial bamboo replaces shed leaves in a short time during early spring (February and March), whereas shedding of old leaves and growth of new leaves in sympodial bamboo occur during a much longer period from mid-winter to mid-summer (December-July with a peak in March/April). Aging particularly affects the transport tissues of bamboo culms, which lose their conductivity for water, nutrients, and photosynthates over the years. The photosynthetic capacity of bamboo leaves decreases with age as well but this has different consequences in monopodial and sympodial bamboos. The reason for this is the difference in life span of leaves in the two groups. Life span of leaves of monopodial bamboos is no more than 2 years, whereas that of sympodial bamboos is up to 6 years. Age of all leaves on a culm of a particular age is the same (either 1 year or 2 years) in monopodial bamboos, whereas that in sympodial bamboos is variable (on average 2-5 years). Monopodial bamboos shed only their 2-year-old leaves every year, which can cause a dramatic decrease in leaf area, photosynthesis, and consequently shoot/culm production. "Alternation," when the stand is composed of relatively more culms with 2-year-old than 1-year-old leaves, causes marked biennial variation in growth of monopodial bamboos. This does not happen in sympodial bamboos where the photosynthetic capacity of foliage of culms aged 2 years and over is much reduced due to the older age structure of leaves on them. This is in contrast to culms of monopodial bamboos, which "refresh" their leaves every 2 years and retain culm productivity longer. Therefore, despite the fact that felling age of culms also depends on their use (i.e., <1 year for edible shoots, 1 year for pulping and papermaking, and >2-3 years for timber), culms of monopodial bamboos can be harvested much later than those of sympodial bamboo. The latter do not contribute much to new growth after about 2-3 years of age. This is indeed reflected in the average felling age of culms, which is 5-6 years for monopodial bamboo and only 4 years for sympodial bamboo.

The exceptionally rapid flush of growth of belowground shoots and aboveground culms requires net-import of energy and nutrients. In contrast to older interpretations of remobilization and translocation from stored reserves in rhizomes, newer studies indicate that the greater part of carbohydrates required for new shoot and culm growth originates from current photosynthesis by leaves on older culms. Also the greater part of nutrient ions originate via absorption from the soil during the shoot season. This has clear implications for managing the environment in relation to providing sufficient resources, i.e., nutrients (and water) during this period. Indeed, most "recommendations" for nutrient application in bamboo suggest applying 1 month before shoots appear aboveground; a second application during rhizome growth is also sometimes recommended. Nutrient application rates average 318, 149, and 126 kg/ha/year of N, P, and K. When compared with average contents of those nutrients in plants, it appears that K rates are much too low, whereas P rates are too high. Data for average fertilizer-use efficiency of applied N, P, and K follow the same pattern as average nutrient content of plants: K>N>P.

Unregulated exploitation of stands is a major reason for degradation of bamboo resources worldwide. Harvesting of very young culms for fiber or timber has jeopardized bamboo growth since ancient times, e.g., in China, but more recently inappropriate harvest has lead to extremely low and extremely high standing-culm densities. If bamboo stands are left undisturbed, biomass production increases until aboveground and belowground competition results in decreasing annual rates of biomass gain. Control of standing-culm density is the most important measure to combat such a decline in productivity. Appropriate densities vary dramatically depending on the product(s) for which bamboo is cultivated. These average 7,400, 9,100, and 13,300 standing-culms per hectare for shoot-only, shoot and timber, and timber-only bamboo stands, respectively. Variations from these averages are due to species differences (higher density for species with thinner culms), yield (higher density for greater total yields), shoot and culm quality (lower density for thicker shoots and culms), and production sites (higher density to maximize yield in "poorer" sites and lower density to maximize quality in "richer" sites).

To sustain not only the productivity of perennial bamboo but also maintain the productivity of its growing sites, management of the soil is of paramount importance. Bamboo will grow under soil conditions which are not suitable for other crops. Therefore, they are widely used for rehabilitation of degraded land. During commercial production, harvest and management conditions result in soil disturbance, which stimulates a chain reaction that reduces total soil content of nutrients, and increases nutrients in the labile fraction of soil biomass and finally in the mineralized form (Silgram and Shepherd, 1999). Exclusive application of inorganic fertilizers has the same effect and, therefore, adding organic fertilizers to bamboo is required. Part of this organic fertilizer is self-provided in the form of bamboo litter: on average, about 8 t/ha of biomass, which is approximately 7% of the total biomass of plants including 63, 6, and 42 kg/ha of N, P, and K are annually recycled in bamboo stands. Decomposition is slower in temperate climates (up to 6 years) than in tropical climates (2-3 years). Addition of organic mulches may help to maintain soil organic matter and manipulate soil temperature and soil moisture, and reduce solar radiation incidence at the base of bamboo stands.

In conclusion, the present understanding of bamboo growth patterns and their management, and of management of the bamboo growth environment, provides the technical basis for concerted efforts to raise productivity, and the supply of bamboo products across both temperate and tropical climates.

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