

## Ecological position, structure, and diversity of the groves of the Giant Bamboo, *Phyllostachys pubescens*, in Subtropical China

- Marinus J.A. Werger, Utrecht, Rui Li, Hangzhou, Zhangcheng Zhong, Beibei, Heinjo J. During, Utrecht -

### Summary

The giant bamboo, *Phyllostachys pubescens*, is widely planted in the subtropical evergreen broadleaved forest zone of China, Taiwan and Japan. It is of great economic importance, for its poles and even more so for its young shoots which are a vegetable delicacy, and in China alone *Phyllostachys pubescens* groves cover some 3 million hectares. This bamboo has been cultivated and harvested for thousands of years. Stands commonly produce new shoots, in March/April, in a remarkable, strongly alternating pattern of 'on-years' (with a high production of new shoots) followed by 'off-years' (with a low production of new shoots). Production of new shoots varies between years by a factor 10 or more. This alternative production between years has, to our knowledge, never been properly explained, though depletion of reserves stored in the rhizome system in the 'on-year' by the great number of new shoots, and slow replenishment afterwards, has been suggested to cause the rhythm.

We discovered that the alternation between 'on-years' and 'off-years' is caused by the peculiar leaf phenology of this species in combination with a disparity in the age structure of the population of bamboo culms. Leaves on the newly emerged culm are all shed after one year and subsequent leaf cohorts always are shed after two years. Young leaves have very much higher photosynthetic rates than old leaves, and the production of new shoots is strongly related with the number of culms with young leaves. If once a disparity in the culm population of the stand is created between culms with young leaves, as against culms with old leaves, this leads to the rhythm of years with many new shoots alternated by years with few new shoots. The pattern of leaf phenology reinforces that rhythm. The proportion of emerging culms reaching maturity (20 %) does not differ between years. The rest dies soon after emergence. New shoots grow up to the canopy of 12 to 20 m high within 4 to 6 weeks, we recorded height growth of up to 98 cm per 24 hours.

Secondary succession on patches of logged-over evergreen broad-leaved forests in this subtropical zone starts with a species-poor (ca. 30 species) grass - herb vegetation in which light-demanding pioneer pines (often *Pinus massoniana*) invade and build an open pine forest. In the open pine forest gradually the broad-leaved evergreen species become established and form a dense canopy under which the pines cannot rejuvenate. If left untended, *Phyllostachys pubescens* groves also regenerate into subtropical evergreen broad-leaved forest, but the pine stages are skipped: the succession starts directly with establishment of the evergreen broad-leaved species. In Sechuan, South Central China, the climax vegetation is a species-rich (ca. 120 - 140 species) *Castanopsis fargesii* - *Elaeocarpus japonicus* forest on mesic and mesotrophic to nutrient-rich sites, and a species-poorer (ca. 50 - 70 species) *Schima argentea* - *Gordonia acuminata* forest on drier sites. This succession takes about one to two centuries.

Dominance - diversity curves in this succession series are initially geometric, indicating pre-emption of resources at similar fractions per species (competition for light), but gradually develop into the common log-normal curves, indicating competition for several resources.

## Zusammenfassung

Der Riesenbambus *Phyllostachys pubescens* wird großräumig in der subtropischen Zone von China, Taiwan und Japan, wo normalerweise immergrüner Wald wächst, angepflanzt. Die Art hat großen wirtschaftlichen Wert und liefert Pfähle und eine delikates Gemüse. In China alleine bedeckt diese Art über 3 Millionen Hektar. In China hat man diesen Bambus seit Jahrtausenden kultiviert. Er produziert seine neuen Sprosse im März/April, meistens in einer auffälligen Sequenz von einem 'guten Jahr', in dem es viele neue Sprosse gibt, abwechselnd mit einem 'schlechten Jahr', in dem sehr viel weniger neue Sprosse produziert werden. Der Unterschied zwischen guten und schlechten Jahren kann um dem Faktor 10 variieren. Dieser bemerkenswerte Wechsel der Produktionsjahre ist, soweit uns bekannt, nie eindeutig erklärt worden. Wir haben entdeckt, dass der Rhythmus von der eigenartigen Blattphaenologie von *Phyllostachys pubescens* in Zusammenhang mit einer ungleichen Altersstruktur der Bambussprosse in der Population verursacht wird. Die Blätter an den neu herauswachsenden Sprossen werden nach einem Jahr abgestoßen; alle weiteren Blattkohorten bleiben jeweils zwei Jahre am Spross. Die jungen Blätter haben eine viel höhere Photosynthese-Rate als die alten. Die Produktion von neuen Sprossen ist stark korreliert mit der Anzahl der voll ausgewachsenen Sprosse mit jungen (bis zu einem Jahr alten) Blättern. Wenn aus irgendwelchem Grund in einer Population einmal die Anzahl der Sprosse mit jungen Blättern abweicht von der Anzahl der Sprosse mit alten Blättern, so führt dies unwiderruflich zum obengenannten Produktionsrhythmus. Das blattphaenologische Muster verstärkt diesen Rhythmus. Der Prozentsatz der Neusprosse, die weiterhin voll ausgewachsen (20 %), ist von Jahr zu Jahr stabil. Die übrigen 80 % sterben bald nach Erscheinen ab.

Neusprosse wachsen innerhalb von 4 bis 6 Wochen in das 12 bis 20 m hohe Kronendach hinein; wir haben Wuchsgeschwindigkeiten bis zu 98 cm in 24 Stunden gemessen.

Die Sekundärsukzession in abgeforsteten Flächen im subtropischen immergrünen Wald in dieser Region fängt mit einer artenarmen (ca. 30 Arten) Gras-Kräuter-Flur an, worin sich bald lichtbedürftige Pinien (oft *Pinua massoniana*) ansiedeln, die einen offenen Wald bilden. In diesem Pinienwald siedeln sich dann die immergrünen Holzgewächse an und regenerieren zum immergrünen breitblättrigen Wald. In vernachlässigten *Phyllostachys*-Beständen führt die Sukzession auch zu immergrünem breitblättrigem Wald, aber hier wird das Pinienstadium übergangen: die immergrünen Arten dringen direkt in den Bambusbestand ein. In Sechuan, Süd-Zentral China, ist die Klimaxvegetation auf mäßig feuchten mesotrophen Böden ein artenreicher (ca. 120 - 140 Arten) *Castanopsis fargesii* - *Elaeocarpus japonicus* Wald und an trockeneren Stellen ein etwas weniger reicher (ca. 50 - 70 Arten) *Schima argentea* - *Gordonia acuminata* Wald. Diese Sukzessionsserie braucht ungefähr ein bis zwei Jahrhunderte. Die Dominanz - Diversitätskurven in dieser Sukzessionsserie sind am Anfang geometrisch, deuten also auf eine starke einseitige Konkurrenz um Licht, werden jedoch später in der Sukzession Log-Normal-Kurven, was auf eine vielseitigere Konkurrenz hinweist.

## Latitudinal und altitudinal position

China is a vast country spanning an enormous variety of climatic zones: from the seasonal, cold-temperate areas in the northeast with boreal needle forests, to the moist, tropical parts in the southeast with rain forests; and to the dry and semi-arid regions in the west, where

lowlands as well as high mountain areas occur, supporting desert and high-mountain steppes (Fig. 1).

The subtropical zone covers about 25 % of the surface area of China. It reaches up to about 30 degrees northern latitude (locally even to 33 degrees north), and is still under the influence of the western Pacific monsoons. This influence has a seasonal pattern: the warm and humid, oceanic air masses prevail in the very south of China during most of the year. In spring they move northwards into the inland area and reach the Yangtze River around April. In June they have crossed the Yangtze valley, bringing rain also further north (GUO 1999, FANG 1988). In winter the areas south of the Yangtze River do not receive much precipitation, though air humidity stays relatively high and fogs are frequent. Temperatures, at least at low elevations, are not often and never drastically below zero (Fig. 2).

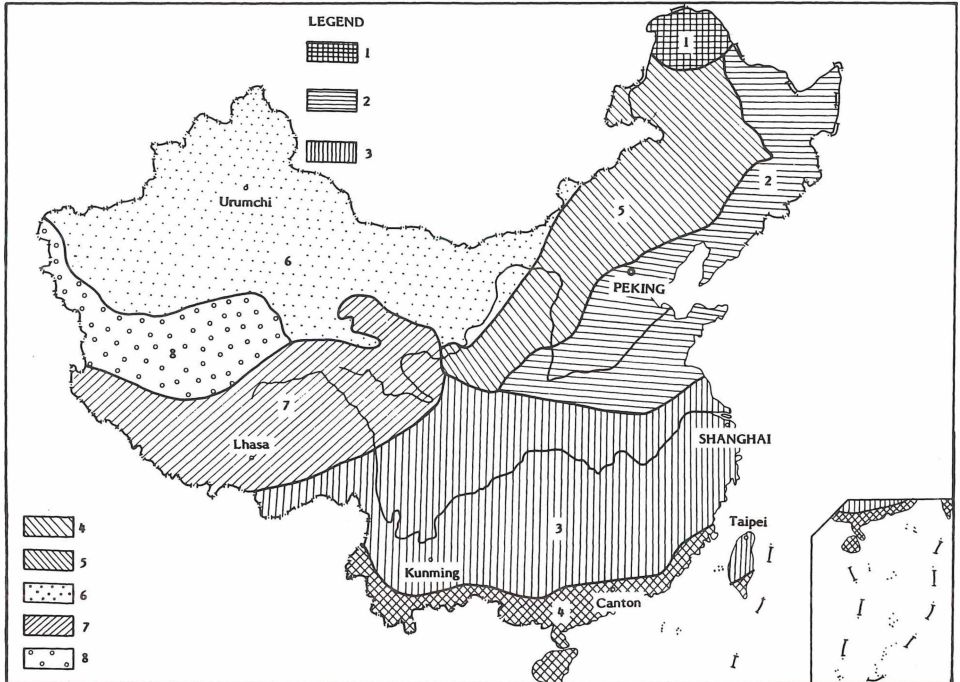


Fig. 1: Map of China showing the vegetation regions: 1. Cold-temperate deciduous needle-leaved forest, 2. Temperate deciduous broad-leaved forest, 3. Subtropical evergreen broad-leaved forest, 4. Tropical seasonal rain forest, 5. Temperate steppe, 6. Temperate desert, 7. High-cold meadow and steppe, 8. High-cold semi-desert and desert. (from HOU 1983).

The vegetation in this subtropical zone is typically a subtropical evergreen broad-leaved forest. SONG (1983, 1988), LIU (1988) and ZHONG (1988) give useful descriptions of the forests in this subtropical zone. There are some conspicuous differences in climatic conditions and in species composition of the forests of the subtropical zone of the eastern as compared to the more central Chinese areas.

Above an altitude of about 1600 m in the south of this zone (and above 1100 m further north), the forest contains evermore broad-leaved deciduous species, particularly in the forest canopy, and transgresses into a deciduous broad-leaved forest (WU et al. 1980, GUO 1999, TANG & OHSAWA 1997). A similar gradient is found in northern direction (Fig. 3).

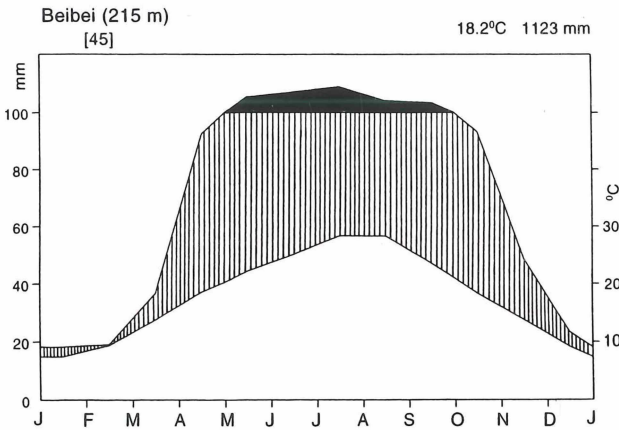


Fig. 2: Climate diagram of Beibei, Sichuan, based on data collected from 1951 till 1995 by the meteorological Station Beibei. Scales and legends follow WALTHER & LIETH (1967).

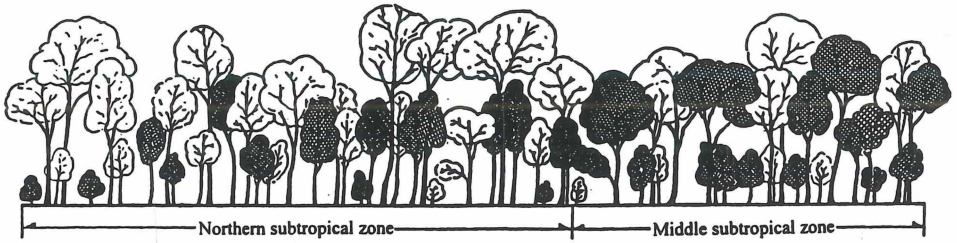


Fig. 3: Latitudinal transect from the mid-subtropical zone to the northern subtropical zone in East-Central China, showing the increase in abundance of deciduous species {white crowns} and the decrease in abundance of evergreen tree species (hatched crowns) and their evermore limited tree height in northern direction (adapted from WU et al. 1980 and GUO 1999).

### Floristic composition

Generally the tree flora of these forests is very rich in species and contains many rare species of limited distributional range, including 'relict species'. Most of the species are either of tropical affinity or have Sino-Japanese distribution areas. Typical tree composition in these forests is as follows: At lower elevations Lauraceae, Symplocaceae, Hamamelidaceae, Theaceae, Elaeocarpaceae and evergreen Fagaceae abound; at medium elevations Lauraceae and Theaceae are still important but represented by other species, while Magnoliaceae and Fagaceae become more frequent; and at higher elevations Theaceae and Symplocaceae still occur but Ericaceae are frequent. Leaves are mainly simple and leathery (SONG 1983,1988; ZHONG & MIAO 1986; ZHONG 1988; TANG & OHSAWA 1997; GUO 1999).

The life form spectra of these forests shows that the understorey is fairly rich (up to around 20 %) in hemicryptophytes, but largely these are hemicryptophytic species with well-developed belowground storage organs (ZHONG 1988).

However, apart from the steepest and remote mountain areas, the subtropical zone in China is densely populated and has been so for some two thousand years. That implies that the forest vegetation in the valleys and on many of the lower slopes has been very largely removed and most of that area has been taken into agricultural production. At lower and medium elevati-

ons the countryside is mostly covered with rice paddies and other arable fields. Pastures occur nearly solely higher in the mountains. Relatively large areas at lower and medium elevations, mainly on slopes, have been transformed into groves of the giant bamboo *Phyllostachys pubescens*. This species most probably is native to this region. It has been used by the Chinese population for economical purposes since times immemorial: there are proofs of the utilization of bamboos since at least some 7000 yr BP and the oldest book we still have on the cultivation of bamboo dates from 450 AD (HSIUNG 1986, LIAO 1990, LI 1998).

### ***Phyllostachys pubescens* groves**

*Phyllostachys pubescens* is a giant bamboo native in southern China and perhaps Vietnam. Centuries ago it was introduced into Taiwan, Japan (in 1746: ISAGI et al. 1997) and Korea, and throughout this vast region it is a species of great economic importance. Shoots of this species grow up to 12 - 20 m tall, which is about the same height as most of the forest in the area. The bamboo shoots emerge individually from an extensive monopodial rhizome system and build fairly dense stands under natural conditions. Farmers turn those stands into open groves, annually harvesting large numbers of shoots that are 6 to 10 years old. The farmers also periodically remove all regrowth of other woody species in the bamboo groves; only few bamboo groves grow mixed with other trees.

Many groves originate from vegetative parts planted ages ago by the farmers, and the small initial groves gradually spread vegetatively over larger areas.

In China, groves of *Phyllostachys pubescens* are common in the Yangtze area up to 800 m a.s.l. (occasionally up to 1200 m a.s.l.). Groves frequently are 10 000 to 20 000 ha in size, and some are even larger than 100 000 ha. In China alone groves of *Phyllostachys pubescens* cover more than two million hectares.

The economic value of this species was and is its use as timber, pulp, and, increasingly so, the consumption of its young sprouts as a delicatessen vegetable. Up to the 1980s the yield of *Phyllostachys* poles in China was up to about 10 tons per ha per year, and the yield of vegetable shoots up to 25 tons (fresh weight) per ha per year (Hsiung 1986).

### **Stand structure**

The giant bamboo *Phyllostachys pubescens* produces shoots of 10 to 20 m high. They grow out from an extensive monopodial rhizome system. New shoots grow out in spring and reach a natural age of 10 to 14 years (Fig. 4). Shoots reach their final height within 7 to 10 weeks. Shoot strength and number of branches and second and third order branches increase during the first few years after emergence, and shoot stem colour changes from blue-green to green as the shoots get older (UEDA 1960, NUMATA 1979)

In Sichuan, China, we measured mature shoot densities of 22 - 45 shoots per 100 m<sup>2</sup> (LI 1998, LI et al. 1997a,b,c, 1998a,b,c, 1999), and in Japan, in stands that are not logged, shoot densities are about twice as high (SUZUKI 1987, ISAGI et al. 1997). Shoot diameters at breast height (DBH) range from 6 to 16 cm and DBH generally is a good predictor of bamboo shoot height (WATANABE et al. 1989). Branching along the shoots starts at ca. 4 -5 m aboveground. Branches are positioned in about 30 tiers, alternately attached at the nodes along the stem. Branch lengths and branch angles follow a spatial pattern that results in an elliptic foliage distribution over the shoot's crown. This architecture may reduce light competition within and between the shoots in the grove (LI 1998, LI et al. 1999). In China, Leaf Area Index (LAI)-values are reached of 8.2 m<sup>2</sup>.m<sup>-2</sup> while light intensities at ground level remain surprisingly high at 13 - 17 % of Photosynthetically Active Radiation (PAR) available above the grove's canopy (LIU et al. 1988). In Japan LAI-values of up to about 12 m<sup>2</sup>.m<sup>-2</sup> were found in

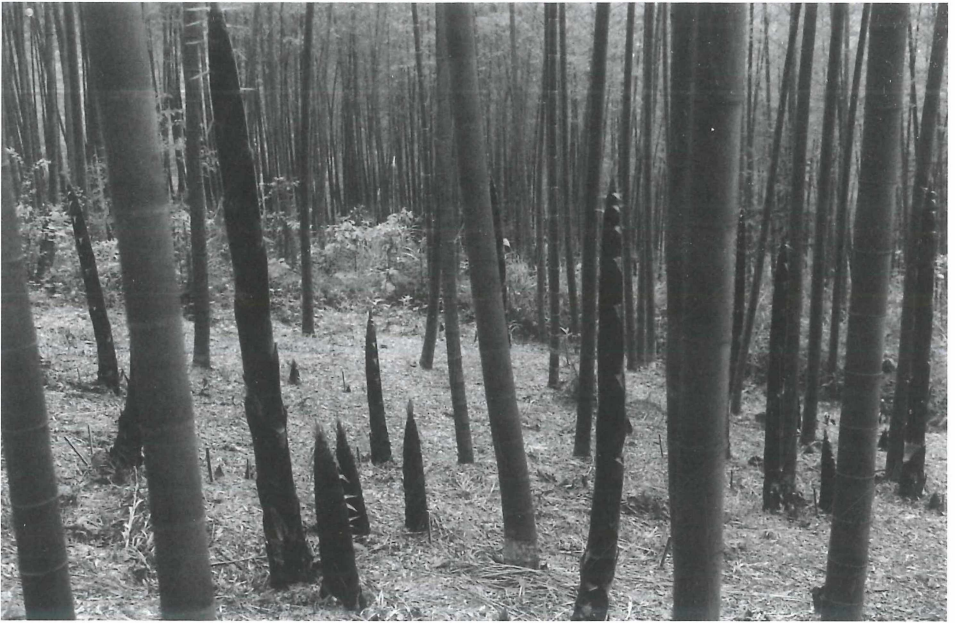


Fig. 4: Grove of the giant bamboo *Phyllostachys pubescens* on Mnt Jinyun, Beibei, Sichuan, in April. The foreground has been cleared of undergrowth by local farmers. The short, darkly coloured shoots are new shoots, tightly wrapped by their dark brown bracts, that have just emerged and started their growth to the canopy. On warm days these shoots may grow about 100 cm in height per 24 hours.

denser, and presumably darker *Phyllostachys pubescens* groves; this value of LAI was highest among 'forest types' (SUZUKI 1987, ISAGI et al. 1997).

In our plots, with a mature shoot density of 39 shoots per 100 m<sup>2</sup>, we measured aboveground biomass values of 61.9 tons per ha, and belowground biomass values of 69.9 tons per ha. The average belowground:aboveground ratio was thus 1.13. This value is affected by the annual harvesting of aboveground material of about 10 - 15 % of the standing aboveground mass (6 to 10 year old shoots are annually harvested) (LI 1998, LI et al. 1998b, 1999). In a *Phyllostachys pubescens* grove in Japan that was not harvested for at least 20 years ISAGI et al. (1997) measured an aboveground biomass of 137.9 and a belowground biomass of 44.6 tons per ha, which makes a belowground:aboveground ratio of 0.32. Of the aboveground biomass about 80 % is in stems, 15 % in branches, and 5 % in leaves. In the belowground biomass, rhizomes (44 %) and thick roots (25 %) are the most important components. About 90 % of the belowground biomass is found in the uppermost 30 cm of the soil. In some studies this is down to 50 cm (LI 1998, LI et al. 1999, UEDA 1960, ISAGI et al. 1997). Individual functional rhizomes extended over tens of meters, and the average rhizome section between ramifications was 2.6 m. Per 1 m<sup>2</sup> soil we found about 6.9 m of rhizome (LI 1998, LI et al. 1999)

The production of aboveground biomass varied strongly from year to year: we measured 12.9 tons per ha per yr in a 'good' year as against 2.1 tons per ha per yr in a 'poor' year (see below). Below ground net production was about 6.6 tons per ha per yr (LI 1998, LI et al. 1998b, 1999). This is comparable to values found in Japan (ISAGI et al. 1997).

## Leaf phenology and Growth

In the literature *Phyllostachys pubescens* is listed as being evergreen, and casual inspection of the groves give the impression of evergreenness. We have discovered, however, that *Phyllostachys pubescens* is not evergreen, but has an intriguing leaf phenology. The new shoots that emerge in March, April each year reach the top of the canopy by the end of May or early June and subsequently drop their sheath bracts and grow branches and leaves. These leaves stay on the shoot for approximately one year and are dropped the next April. Within weeks these bare shoots grow new leaves and those leaves stay alive on the shoots for two years; then they are dropped. Each subsequent crop of leaves maintains this two-year life cycle. We also discovered that this peculiar leaf life cycle explains the strong alternation of a 'good' year, in which many new shoots emerge, followed by a 'poor' year, in which few new shoots emerge, and so on. The production of shoots varies between years by a factor 10 to 12. This alternation is characteristic for most groves of *Phyllostachys pubescens*, and has been observed since centuries, but it has not been properly explained. Traditionally, the biennial rhythm in shoot production is explained as resulting from the depletion of reserves stored in the rhizome system in the 'on-year' by the great number of new shoots, and its slow replenishment afterwards, similar to the fruit production rhythm in fruit trees of the temperate zone. But this explanation is not correct. We provide the proper explanation below.

Late every summer some lateral buds are activated, mainly on 2 to 6 year old rhizomes. These activated buds produce new shoots which emerge aboveground the following spring (March, April). These shoots start to elongate, mostly at a fast rate, and the rate seems to be positively correlated with prevailing air temperature. Shoot extensions of around 1 m per 24 hours are normal (Li 1998) and the highest value recorded is 119 cm per 24 hours (UEDA 1960). Height growth during the day time is about 1.4 times that during the night time (UEDA 1960, Li et al. 1997a). These highest elongation rates are achieved around the sixth week after the first new shoots emerged. Quite a number of new shoots stop their elongation at an early stage and are subsequently going to die; by the end of April it is clear which shoots in the cohort are going to survive and make it to the top of the canopy and which shoots are dying. Apart from the elongation rates there are a few other characteristics by which dying new shoots are characterized, e.g. they stop guttating in the green tips of the brown sheath bracts which normally are tightly wrapped around the emerging new shoot, and their sheath bracts begin to fit more loosely around the young stem. The farmers recognize these characteristics and harvest these shoots before they die, using them as delicatessen vegetables. Interestingly, it is always a rather constant fraction of the new shoots that die or that survive, independent of the total number of new shoots and of the area: about 80 % die and 20 % survive (ZHOU 1986, Li 1998, Li et al. 1997a,b,c, 1998a).

Around April we have, due to the peculiar leaf phenology of this species, four types of shoots in a grove:

- newly emerged shoots that are elongating and that not yet have grown leaves (new shoots);
- one-year old shoots that are dropping their first crop of leaves and soon will be growing new leaves that are going to last for two years (first-year shoots);
- older shoots that are just dropping their two-year old leaves and will soon be growing new leaves that are again going to last for two years (adults shoots with senescent leaves),
- older shoots that are maintaining their leaves grown in the previous spring and which will last for another year (adult shoots with mature leaves).

It is clear from the characteristic leaf ageing pattern in this species, that the cohort of first-year shoots in the next year will join the category of adult shoots with mature leaves.

When a grove has developed under constant conditions, it may be expected that the number of adult shoots with senescent leaves in the grove is equal to the number of adult shoots

with mature leaves. It is possible, however, that the number of adult shoots with senescent leaves in a grove is changed and no longer is equal to the number of adult shoots with mature leaves. This can be achieved, e.g. by unequal harvesting from the two categories of adult shoots, or because of incidental unequal mortality in the two categories of adult shoots resulting from a sporadic frost, or when an insect plague eats away all bamboo leaves in a grove and thus forces the shoots to start their new two-year leaf cycle in the next season, etc. If in such a particular grove the number of adult shoots with mature leaves does no longer equal the number of adult shoots with senescent leaves, this inequality in shoot numbers per shoot category will perpetuate itself due to the two-year life cycle of the leaves: The shoot category with senescent leaves and that with mature leaves will contain high or low numbers of shoots in a cycle of annual alternation.

We have demonstrated that in groves the number of newly emerging shoots in March, April is strongly correlated with the number of adult shoots with mature leaves, and is not correlated with the number of adult shoots with senescent leaves (LI 1998, LI et al. 1997a,b,c, 1998a,b). This is due to the fact that the leaves when young (up to maturity) have a photosynthetic productivity that is up to about three times higher than that of leaves in their second year (HUANG et al. 1989). The higher photosynthetic productivity of the younger leaves results from their much higher nitrogen concentrations compared to older leaves, and it temporally leads to much higher contents of non-structural carbon (sugar) in the rhizome system in years with relatively many adult shoots with mature leaves (LI 1998, LI et al. 1998b). The strong correlation between the number of newly emerging shoots and the number of adults shoots with mature leaves (with their much higher photosynthetic productivities) explains why the alternate cycle of 'good' and 'poor' years develops in groves with a disparity in the categories of adult shoots and why this cycle may be reinforced in subsequent years: As said before, each spring the first-year shoots shed their one-year-old leaves and the join and reinforce the cohort of adults with senescent leaves. They thus join the cohort of adult shoots that contributed most strongly to their emergence.

At Mt Jinyun, Sichuan, in about 30 ha of *Phyllostachys pubescens* grove at 800 m a.s.l. (Fig. 4), with adult shoot densities of about 25 shoots per 100 m<sup>2</sup>, we found that the numbers of emerging new shoots varied from 42.4 to 3.6 in yearly alternation. In none of the years of observation the number of emerging shoots did correlate with the number of adult shoots, or with the number of adult shoots with senescent leaves, but each year it highly correlated with the number of adult shoots with mature leaves. Each year about 20 % of the emerging shoots survived and grew up to the canopy. Their DBH varied between 8.2 and 10.9 cm. The ultimate height and DBH of the earliest emerging and surviving new shoots in a cohort were slightly larger than those of somewhat later emerging and surviving new shoots in the same cohort (Fig. 5). The new shoots emerged in a significantly clumped pattern of 1 - 2 m away from the adult shoots with mature leaves, but relative to all adult shoots, or to the adult shoots with senescent leaves, the pattern of emergence was random. Clearly, activated buds proximal to adult shoots with mature leaves have a better chance of producing an emergent new shoot and of subsequent survival than more distal buds. Dirichlet tessellation showed that there was no significant difference in 'tile size' between the surviving and non-surviving new shoots, which suggests that mortality of the new shoots is density-independent (LI 1998, LI et al. 1997a,c, 1998c). Mortality, or survival, apparently is also not light-dependent but the number of emerging new shoots formed on a rhizome decreases markedly with rhizome age (UEDA 1960).

Fertilization (with NPK) significantly increased the number of emerging new shoots depending on the amount of fertilizer added but survival remained at about 20 %, and the annual alternation in total numbers was not suppressed. While fertilization led to a slightly earlier emergence of the new shoots, it did not increase their growth rate nor their size (LI 1998, LI et al. 1998b).



Stands of *Phyllostachys pubescens* have been reported to flower about once in 60 - 70 years, but there are few records and the period before flowering may be much shorter (NUMATA 1979, WATANABE et al. 1982, LIAO 1990). UEDA (1960) reported that flowering in *Phyllostachys pubescens* is rare, and that flowering occurs at the time of leaf shedding. In some cases all shoots on the same rhizome may flower one after the other in the same year and this will lead to the death of that rhizome. In other cases limited patches in a grove (up to 6 %) flower, each year another patch in a consecutive series of 5 to 10 years. After flowering these patches die. The seeds are ripened and dropped in the year of flowering and usually germinate the same year. After 2 - 3 years the seedlings develop new rhizome systems. However, when flowering is patchy, the openings in the grove are mainly filled by vegetative growth of rhizomes from the neighbourhood (LIAO 1990).

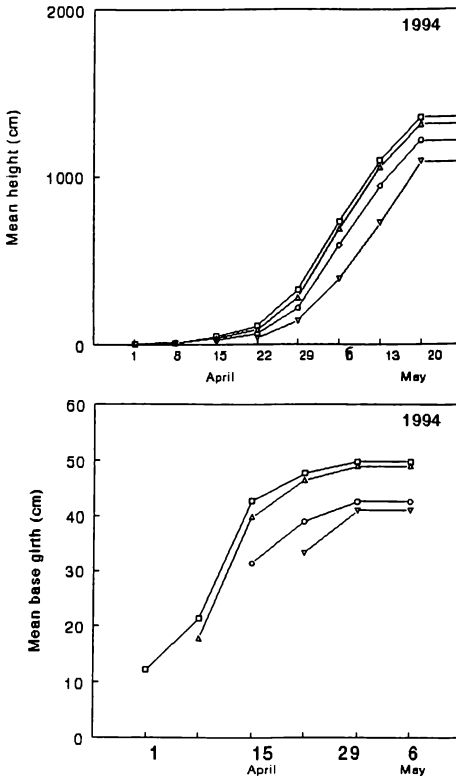


Fig. 5: Emergence and growth of new shoots of *Phyllostachys pubescens* on Mnt Jinyun, Beibei, Sichuan, in 1994. Data are given as averages for shoots that emerged in a particular week. The horizontal axis gives the time of the year. The vertical axis in the top figure gives the mean height (in cm) of the shoots that emerged in a particular week, and in the bottom figure the mean circumference (girth) (in cm) at the base of the shoots that emerged in a particular week. Note that later-emerging shoots stay thinner and shorter.

### Succession and Diversity curves

When the subtropical evergreen broad-leaved forest is destroyed, succession typically starts with a grassy pioneer vegetation composed of light-demanding species. At a second stage light-demanding pine species invade (typically *Pinus massoniana* or *Pinus yunnanensis*), later followed by more shade-tolerant species that gradually start to dominate in the later stages of succession. In smaller clear-felled patches inside the climax forest, succession starts

with a mixture of those light-demanding pioneer species and the shade-tolerant later-successional species (CORNELISSEN 1993). When the forest is cleared and *Phyllostachys pubescens* is planted, the vegetation in the bamboo groves is not stable. Grasses, ferns and hemicryptophytic geophytes (particularly *Iris japonica*) abound and shade-tolerant later-successional woody species establish themselves in the undergrowth (FLIERVOET et al. 1989). Those woody species are frequently removed by the farmers to keep the grove's understorey open. The light-demanding *Pinus massoniana* does not establish itself in the bamboo groves; apparently the relatively high light levels at ground level are still too low for this species. MIAO & LIU (1988) described the successional development from pioneer vegetation to evergreen broad-leaved climax forest at Mnt Jinyun, Sichuan. Succession starts with a grassland vegetation dominated by *Imperata cylindrica*, accompanied by a number of other grasses and herbs, some weedy, but also a number of seedlings of woody species, most importantly of *Pinus massoniana*. Soon the pines grow taller and dominate the vegetation. The pine forest is usually rather open, with trees up to 12 - 18 m tall, and some herbs and shrubs in the undergrowth and many saplings of evergreen broad-leaved species invading. *Pinus massoniana* itself has increasingly more difficulty in regenerating in this forest stage. After some 50 to 80 years the pines in the forest, while still the tallest trees, decline as the evergreen broad-leaved species, having grown up to the canopy, acquire dominance. Important tree species in this 'mixed forest' are *Gordonia acuminata*, *Rhododendron stamineum*, *Symplocos setchuanensis* and *Ilex triflora*. From then on the climax forest develops. On exposed slopes with frequently drier soils, after some 200 years of undisturbed growth, we find an evergreen broad-leaved *Schima* forest, with *Schima argentea*, *Neolitsea glauca*, *Lindera kwantungensis*, *Castanopsis carlesii*, *Rhododendron stamineum* and *Daphniphyllum oldhamii* as important tree species. On the better sites with richer soils the climax forest is a *Castanopsis fargesii*-dominated forest with *Elaeocarpus japonicus*, *Eurya nitida*, *Symplocos setchuanensis*, *Symplocos laurina*, *Beilschmiedia kweichowensis*, *Sloanea leptocarpa*, *Litsea wilsonii*, and many others as important companions.

During this successional series the vegetation strongly increases in species numbers: from an average of 30 species in fully developed stands of the *Imperata*-association, to 50 - 70 species in the 'mixed' and the *Schima*-forest, to about 120 - 140 species in the *Castanopsis*-forest (MIAO & LIU 1988). The number of species in well-developed stands of *Phyllostachys pubescens* groves is about 30 - 45 (FLIERVOET et al. 1989).

Dominance-diversity curves from the successional series (Fig. 6) are geometric for the pioneer stage, but turn to log-normal distributions in the following stages, including the *Phyllostachys* groves (MIAO & LIU 1988, FLIERVOET et al. 1989). The geometric distribution of the ranking of species importance values in a stand commonly has been interpreted as an indication of the prevalence of the process of resource pre-emption in that stand: A number of species all compete predominantly for the same resource (in this case most probably 'light') and 'exhaust' a similar proportion of that resource, in the sequence of their dominance. The log-normal distribution would indicate that most species compete with different success for several different resources, while the short linear sections formed by some sets of species along those log-normal dominance-diversity curves might indicate the development of different guilds of species (SUGIHARA 1980).

We thus see that in the subtropical zone of China the evergreen broad-leaved forest has been cleared away and, over rather large areas, been replaced by groves of the giant bamboo *Phyllostachys pubescens*. These groves are cultivated by the local farmers and have a high economic value. The giant bamboo has a unique rhythm of leaf phenology, and we have unravelled how this rhythm can lead to the remarkable annual variation in the production of new bamboo shoots, that has been reported since centuries. Floristically, the bamboo groves can

be regarded as an early successional stage in the regeneration process towards evergreen broadleaved forest. If left undisturbed, the groves will eventually regenerate into such a subtropical evergreen broad-leaved forest.

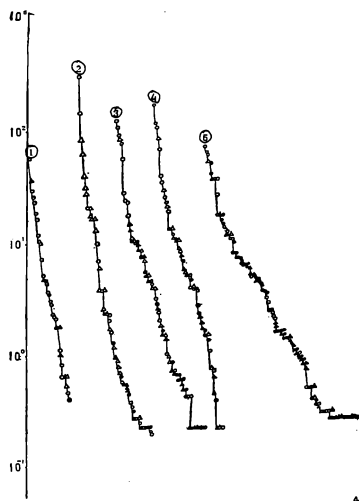


Fig. 6: Dominance-diversity curves from the successional series in the subtropical evergreen broad-leaved zone in Sichuan: 1. *Imperata*-association, 2. *Pinus massoniana*-forest, 3. 'mixed' forest, 4. *Schima*-forest, 5. *Castanopsis*-forest. (from MIAO & LIU 1988).

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Prof. Dr. Marinus J.A. Werger, Heinjo J. During, Dept. of Plant Ecology, Utrecht University, P.O. Box 80084, 3508 TB Utrecht, The Netherlands

Rui Li, Dept. of Geography, Zhejiang University, Hangzhou, 310028 China

Zhangcheng Zhong, Dept. of Biology, Fac. of Life Sciences, South West China Normal University, Beibei, Chongqing, 400715 China

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During Hein Johannes

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