

Interactions Between Shoot Age Structure, Nutrient Availability and Physiological Integration in the Giant Bamboo *Phyllostachys pubescens*

R. Li^{1,2,3}, M. J. A. Werger¹, H. de Kroon⁴, H. J. During¹, and Z. C. Zhong³

¹ Department of Plant Ecology and Evolutionary Biology, University of Utrecht, Utrecht, The Netherlands

² Department of Resources and Ocean Engineering, Hangzhou University, Hangzhou, China

³ Department of Life Science, Southwest China Normal University, Chongqing, China

⁴ Plant Ecology and Nature Conservation group, Department of Environmental Sciences, Agricultural University, Wageningen, The Netherlands

Received: December 10, 1999; Accepted: May 23, 2000

Abstract: The age structure of adult shoots, the nutrient availability of the habitat, and their interaction, are important factors influencing the productivity of bamboo groves. In a field fertilization experiment over two years we examined the impact of physiological integration on the emergence, growth, and survival of new shoots of *Phyllostachys pubescens*, a giant woody bamboo. Impacts of physiological integration were compared using uniform and patchy fertilization treatments. The number of new shoots emerging per plot significantly increased with the application of fertilizer (NPK), but the increase was constrained by the age structure of adult shoots. In a year with a high proportion of shoots with new (first-year) leaves many more new shoots emerged than in a year with a low proportion of new leaves. Mean survivorship of the new shoots was constant at 20% for all treatments in both years of study. Surprisingly, fertilization did not increase DBH or height of the new shoots, suggesting that shoot size was fixed early in ontogeny. The pattern of fertilizer application, either uniform or patchy, did not affect the total number of new shoots produced. In the case of patchy application, more new shoots developed in unfertilized patches in comparison to uniformly unfertilized plots, probably because these parts of the clone received resources via the rhizomes from the adult shoots in adjacent fertilized patches. The production of new shoots in fertilized patches, in turn, was lower than that in uniformly fertilized plots as a result of this physiological integration. The results are discussed in the general context of the impact of integration on clonal plant performance in dense stands.

Key words: Age structure, bamboo, clonal growth, patchy fertilization, physiological integration, vegetative reproduction.

Introduction

Physiological integration refers to the exchange of resources and growth substances between interconnected ramets of a clonal plant (Marshall, 1990^[26]; Pitelka and Ashmun, 1985^[29]). Integration is a fundamental process influencing the perform-

ance of many clonal plant species (Alpert and Stuefer, 1997^[11]; Jónsdóttir and Watson, 1997^[18]). Two situations in particular have received attention in recent years. First, in patchy habitats, clonal fragments growing in favourable micro-sites support the growth of the clone in unfavourable micro-sites (e.g., Marshall, 1990^[26]). If the benefits associated with resource import outweigh the costs associated with export, integration is beneficial to the whole plant. Recent evidence suggests that the performance of the entire clone growing in a patchy habitat may exceed the performance in a uniform habitat, even if the total amount of resources supplied in both habitats is the same (Alpert and Stuefer, 1997^[11]; Birch and Hutchings, 1994^[3]; Hutchings and Wijesinghe, 1997^[15]; Stuefer et al., 1996^[33], 1994^[34]). This has been studied only in "foraging" clonal plants that tend to occur in fairly low densities in a matrix of other plants; whether it also applies to clonal plants which themselves form dense, "monoculture" stands, is as yet unknown.

Second, it has been suggested that physiological integration plays a prominent role in shoot demography in clonal species growing in dense monospecific stands (e.g., de Kroon, 1993^[4]; Hutchings, 1979^[13]). Support of small, suppressed shoots in the stands may reduce density-dependent mortality and even prevent self-thinning. While evidence has accumulated that small shoots are indeed supported, it is still a matter of debate as to what extent the shoot demography in dense stands is significantly altered by the process of physiological integration (de Kroon and Kalliola, 1995^[5]; Suzuki and Hutchings, 1997^[35]).

Populations of rhizomatous giant bamboos rely heavily on vegetative reproduction for the recruitment of new shoots, since flowering is a rare event in these species (Janzen, 1976^[17]; Liao, 1990^[23]; MacClure, 1966^[25]). Insight into the factors affecting annual recruitment rates, including the role of physiological integration, is crucial for a better understanding of the dynamics of shoot populations of these species.

Phyllostachys pubescens Mazel is such a giant bamboo. New shoots of this bamboo are produced in early spring. In many stands, years with high numbers of new shoots (up to 3000 per ha) alternate regularly with years with much lower recruitment rates (about 500 per ha; Li et al., 1998b^[20], d^[22]). This pattern appears to be due to the peculiar leaf age structure of

the stand (Li et al., 1998b^[20]). Leaf life span of this bamboo is two years, except in first-year shoots where it is only one year. Two-year-old leaves and leaves on first-year shoots are dropped in April, during the emergence and elongation of new shoots (Bamboo Research Institute of Nanjing Forestry University, 1974^[2]). Flushing of new leaves soon follows upon shedding of the old leaves. Stands with alternating high- and low-recruitment years are characterized by an unbalanced age structure of the adult shoots: the proportion of adult shoots replacing their leaves in, say, even years, differs considerably from that of adult shoots replacing their leaves in odd years (Li et al., 1998b^[20]). The number of recruits is strongly positively correlated with the proportion of adult shoots with one-year-old leaves, which may be related to the fact that the maximum rate of photosynthesis of first-year leaves of *P. pubescens* is up to three times higher than that of second-year leaves (Huang and Yang, 1989^[12]), which corresponds to a higher nitrogen content of first-year leaves (Li et al. 1998d^[22]). Apparently, the new shoots are mainly provided with resources by the adult shoots with one-year-old leaves. The first-year shoots drop their leaves in the next spring, at the same time as the adult shoots which contributed most to their emergence and growth; thus, the many recruits from a high-recruitment year join the cohort of adult shoots which supported their growth, and in this way the imbalance between adult shoots with one- and two-year-old leaves is maintained. Moreover, survival rates of new shoots are about 20% irrespective of the density of recruits (Li et al., 1998b^[20], d^[22]).

The correlation between the number of new shoots and the proportion of adult shoots with one-year-old leaves suggests that the production of new shoots is mainly affected by the carbon budget of the clonal system. On the other hand, it has been found that fertilization with NPK increases the production of new shoots (Bamboo Research Institute of Nanjing Forestry University, 1974^[2]; Shi and Bian, 1987^[30]; Ueda, 1960^[36]). This increase in productivity may mainly result from an increase of leaf photosynthetic capacity, which is positively correlated with leaf nitrogen concentration (Hirose and Werger, 1987^[10]; Mooney, 1986^[27]). The production of new shoots, therefore, seems to be affected by the age structure of adult shoots, nutrient availability, and their interaction.

Although fertilization will increase the production of new shoots in all years, we predict that, as long as the age structure of adult shoots in a bamboo grove remains unbalanced as mentioned above, fertilization will not eliminate the fluctuations between years. In view of the similarity in survival rates in "good" and "poor" years we also expect that fertilization will not affect the survival rate of new shoots. We hypothesize that, if fertilization is applied patchily, clone parts in the unfertilized subplots will perform better (in terms of the number of new shoots and their sizes) than clone parts growing in homogeneously unfertilized control plots. Since export of resources to connected clone parts in adjacent unfertilized subplots inevitably reduces the amount of resources available to parts of clones growing in fertilized subplots, the latter will perform worse than clone parts growing under homogeneously fertilized conditions.

Species and Study Area

Phyllostachys pubescens is a monopodial giant bamboo. It is widely distributed in southern China and the neighbouring countries, Japan and Korea (Bamboo Research Institute of Nanjing Forestry University, 1974^[2]; Isagi et al., 1997^[16]; Ueda, 1960^[36]). The groves under investigation are situated in the Nature Reserve of Jinyun Mountain (29°50'N, 106°26'E), about 40 km north of the city of Chongqing, Sichuan, China. This area is exposed to the East Asian monsoon. Subtropical broad-leaved evergreen forests cover considerable parts of the area. They are interspersed by large groves of *P. pubescens* that are managed by man. The groves have been cultivated for at least 40 years and probably much longer, according to the local people. Physiognomy, floristics, and structure of these groves were described by Liu et al. (1988^[24]) and Fliervoet et al. (1989^[7]). In recent years, the production of new shoots is good in even years (1990, 1992 and so on), but poor in odd years (1991, 1993 and so on) in these bamboo groves. The experimental site was situated in the centre of a several ha large grove at the middle of a slope with inclination of ca. 15°, facing northeast, at ca. 500–600 m a.s.l. The substrate is a quartziferous sandstone. Soils are acid and yellowish. Especially in the cultivated bamboo groves, nutrient availability is low (Fliervoet et al., 1989^[7]), perhaps due to harvesting of leaf litter and bamboo shoots (Li et al., 1998c^[21]).

Mature shoots are widely spaced in the groves, at a density of ca. 22–45 shoots per 100 m². Height of mature shoots often reaches 10–20 m, and diameter at breast height (DBH) ranges from 8 to 16 cm (Bamboo Research Institute of Nanjing Forestry University, 1974^[2]). The aerial shoots are long-lived, persisting aboveground for more than ten years. Rhizomes in the soil are equally long-lived (Bamboo Research Institute of Nanjing Forestry University, 1974^[2]; Numata, 1979^[28]; Ueda, 1960^[36]). The growth of new shoots is strongly seasonal.

Rhizomes crisscross belowground mainly in the top 30 cm of the soil. Rhizome biomass may amount to 12 t·ha⁻¹ and the density of lateral buds may reach 800 000 ha⁻¹. Rhizomes normally maintain connections over tens of metres and remain viable for over 10 years (Bamboo Research Institute of Nanjing Forestry University, 1974^[2]; Li et al., 1998c^[21]; Wu, 1984^[39]; Zhou et al., 1985^[40]). This leads to a complex pattern of large, intermingled clones. Consequently, the size and spatial extent of individual clones can only be determined after extensive excavations, which were not allowed in the (commercially important) groves. Roots are formed at the shoot bases and the nodes of the rhizomes; their length is about 66 ± 3 cm (Li et al., 1998c^[21]).

New shoots are initiated from solitary lateral buds on rhizomes every summer (June–August); they emerge aboveground the following spring (March–April). Many of these new shoots then die, reaching a height of a few dm only, but some (about 20%) survive and grow rapidly (Li et al., 1998b^[20], d^[22]). They attain their full size (> 10 m in height) about two months after emergence, and may elongate up to one metre per day during the period of fastest growth (Ueda, 1960^[36]). Only when the new shoots have almost attained their maximum length, does leaf expansion on these shoots start, indicating that the carbohydrates and nutrients needed for

their construction are provided by the old rhizomes and adult shoots attached via these rhizomes.

A study of the spatial pattern of emerging and surviving new shoots in relation to the positions of the adult shoots showed that both in high-recruitment years and in low-recruitment years, newly emerging shoots were significantly clumped at a distance of 1–2 m away from adult shoots with one-year-old leaves (Li et al., 1998a^[19]). This suggests, that the carbohydrates, needed for the growth of a new shoot, derive mainly from the adjacent adult shoot with one-year-old leaves. Since the vitality of lateral buds in *P. pubescens* decreases from proximal to distal along a rhizome segment (Hsiung et al., 1990^[11]; Zhou et al., 1985^[40]), our previous results also suggest that new shoots positioned most proximally to an adult shoot with one-year-old leaves will preempt the resources from this shoot and thus prevent the growth of more distally placed new shoots (Li et al., 1998a^[19]). This would put restrictions on the degree of support of new shoots over larger distances by physiological integration. Since, however, the density of surviving new shoots is generally lower than that of adult shoots with one-year-old leaves (Li et al., 1998b^[20], d^[22]), some transport beyond the margins of the plots may be expected.

Each June, the surviving new shoots are numbered and permanently marked with coloured paint by the owners. Therefore, it is easy to trace back the year of emergence for each existing shoot. Each year, mainly in autumn and winter, 7–10-year-old shoots are selectively harvested for timber. Almost all these shoots are still alive when harvested.

Methods

The fertilizer was applied in 10 randomized complete blocks in the bamboo grove. Each block was visually homogeneous in environmental conditions. Within each block, five plots of 9 × 9 m were laid out, each receiving a different treatment. The treatments were as follows (see Fig. 1): C, control (no fertilization); H, fertilizing uniformly over the whole plot; L, fertilizing uniformly over the whole plot but with only half the amount of fertilizer used in treatment H; I, fertilizing only in the inner half area of 6.35 × 6.35 m (40.3 m²) of the plot with the same concentration as used in treatment H; O, fertilizing only in the outer half (40.5 m²) of the plot with the same concentration as used in treatment H. Along the borders of fertilized plots, substantial net export of carbohydrates and nutrients to shoots outside the plots might lead to significant edge effects. In order to minimize such effects, the 2 m wide zone close to the boundary of each plot was fertilized with the same concentration as the outer half of the plot (Fig. 1). Accordingly, for treatment C and I the buffer zone enclosing the plots did not receive any fertilizer. The plots were separated from each other by another buffer zone (without fertilization) of at least 4 m.

The amount of fertilizer for treatment H was as follows: N, 400 kg ha⁻¹ yr⁻¹; P, 100 kg ha⁻¹ yr⁻¹; K, 100 kg ha⁻¹ yr⁻¹. Fertilizer was applied in the form of (NH₂)₂CO, CaH₄(PO₄)₂H₂O, and KCl, respectively. The granular fertilizer, in subsequent proportions of 30%, 40% and 30% of the total dosage, respectively, was uniformly added to the surface soil of the plots, three times per growing season: 1) June 1994 and 1995, during the period of activation of the lateral buds belowground; 2) Sep-

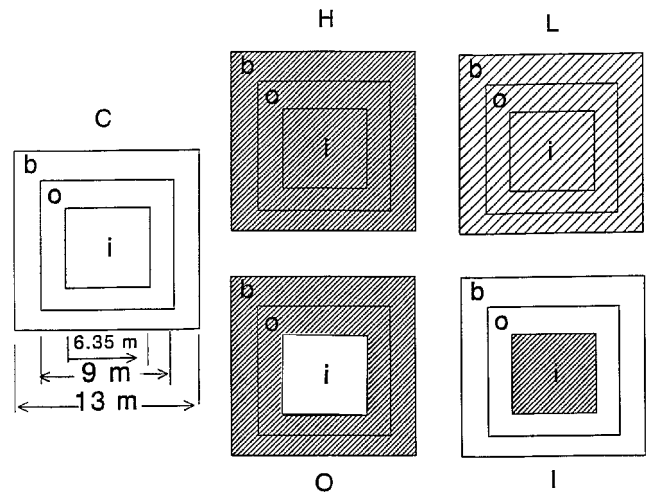


Fig. 1 Nutrient application in treatments within a randomized block. C: unfertilized control; H: uniformly high fertilization; L: uniformly low fertilization with half the dosage of treatment H; I: fertilization of only the inner half (indicated as "i") of the plot; O: fertilization of only the outer half (indicated as "o") of the plot; b: 2 m wide buffer zone that received the same treatment as its enclosed outer half area of the plot. Details on the application of fertilizers are described in the text.

tember 1994 and 1995, in the course of the development of new shoots belowground; 3) January 1995 and 1996, before the emergence of new shoots. The fertilizer was covered by a thin layer of surface soil after the addition. To ensure the fertilizer was effectively absorbed by the bamboo, the understorey shrubs and herbs were uprooted before fertilization. Understorey shrubs and herbs were also uprooted in the control plots.

In each plot, the number of adult shoots was counted, the year of emergence of each adult shoot was ascertained and the diameter (DBH) of each adult shoot was measured at the beginning of March 1995 and 1996.

The new shoots began to emerge aboveground at the end of March each year. To study the effect of the fertilization, censuses at intervals of one or two weeks were carried out from the end of March to the end of May during 1995 and 1996. By the end of May, shoot emergence had stopped and the surviving new shoots had reached the top of the canopy and developed up to their full height and DBH. At each census, the following parameters were recorded: 1) location of each newly emerging shoot (inner or outer half of the plot); 2) height and basal diameter of each new shoot; 3) the fate of each new shoot (surviving or dead). At the last census of each year, the DBH of surviving new shoots was also measured.

A 2-way repeated measure ANOVA was used to test differences in the mean number and individual size of new shoots emerging and surviving per plot between different treatments and different years, and to test differences in the mean number and individual size of adult shoots per plot between different treatments and different years. A 3-way repeated measure ANOVA was used to test the differences in the mean number of new shoots emerging and surviving in the inner or outer half

Table 1 Result of 2-way repeated measures ANOVA tests for mean number of new bamboo shoots per plot and mean individual size of new bamboo shoots in the groves of *Phyllostachys pubescens* with different treatments on Mount Jinyun, Chongqing, China during 1995 and 1996 (see Fig. 2). C: control; H: high fertilization; L: low fertilization; I: (high) fertilization only in the inner half of the plots; O: (high) fertilization only in the outer half of the plots. Significance levels are: **** $0 < p < 0.0001$; *** $0.0001 < p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$; ns: not significant

	Planned comparison	
	# Emerging	# Surviving
Effect of years		
C1995 vs C1996	****	****
H1995 vs H1996	***	*
Effect of fertilization level		
C1995 vs H1995	***	ns
C1996 vs H1996	**	ns
C1995 vs L1995	ns	ns
C1996 vs L1996	ns	ns
L1995 vs H1995	*	ns
L1996 vs H1996	ns	ns
Effect of uniform vs patchy application of the same amount of fertilizer		
L1995 vs (I1995 and O1995)	*	ns
L1996 vs (I1996 and O1996)	ns	ns
Effect of inner vs outer fertilization		
I1995 vs O1995	ns	ns
I1996 vs O1996	ns	ns

area of the plots between different treatments in different years. Within these analyses, the following planned comparisons were carried out to test (cf. Tables 1 and 2):

1. the effects of years: C1995 vs C1996; H1995 vs H1996.
2. the effects of fertilization level in homogeneous plots: C vs L vs H.
3. the effects of uniform vs patchy application with the same amount of fertilizer: L vs (I + O).
4. the effects of treatment of one patch type on the performance in the other patch type in the patchy-application treatments: Ci vs Oi, Co vs Io; Hi vs Ii, Ho vs Oo (see Fig. 1).

Since these contrasts are non-orthogonal, the Dunn-Šidák method was used to correct the significance levels (Sokal and Rohlf, 1995^[31]). The statistical package STATISTICA (StatSoft Inc., 1993^[32]) was used for all calculations.

Results

Adult shoot number and size

There were no significant differences in the mean number of adult shoots per plot, the mean diameter (DBH) and the mean height of the adult shoots, either between different treatments or between different years (data not shown). The number of adult shoots averaged 20–25 shoots per plot of 9 × 9 m for all treatments. Adult shoot density was maintained roughly at the

Table 2 Effects of patchy fertilization in the bamboo groves of *Phyllostachys pubescens* on Mount Jinyun, Chongqing, China during 1995–1996. A 3-way repeated measures ANOVA was used to test the difference in the mean number of emerging new shoots per half plot with different treatments (see Figs. 1 and 4). C: control; H: high fertilization; L: low fertilization; I: (high) fertilization only in the inner half (represented as “i”) of the plots; O: (high) fertilization only in the outer half (represented as “o”) of the plots; Significance levels are: **** $0 < p < 0.0001$; *** $0.0001 < p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$; ns: not significant

Effects	Significance level
Main effects	
Fertilization (F)	****
Year (Y)	****
Patches (P)	*
Interactions	
F × Y	**
F × P	*
Y × P	ns
F × Y × P	**
Planned comparisons	
Effects of import	
Ci1995 vs Oi1995	**
Ci1996 vs Oi1996	ns
Co1995 vs Io1995	ns
Co1996 vs Io1996	ns
Effects of export	
Hi1995 vs Ii1995	*
Hi1996 vs Ii1996	ns
Ho1995 vs Oo1995	ns
Ho1996 vs Oo1996	ns

same level between years by the recruitment of new shoots and the removal of 7–10-year-old shoots by the owner of the groves. The mean DBH and mean height of adult shoots were ca. 10 cm and 12 m, respectively.

Differences between years

During the two growing seasons under consideration, the weather conditions were similar. However, the number of emerging and surviving new shoots was significantly different between the springs of 1995 and 1996. In total, 375 new shoots emerged and 92 new shoots survived in the 50 experimental plots in 1995; 1731 new shoots emerged and 357 new shoots survived in 1996. The magnitude of the increase from 1995 to 1996 was almost the same for different treatments: the numbers of emerging and surviving new shoots in 1996 were about four times higher than those in 1995 (Figs. 2a, b). The DBH and height of surviving new shoots were not significantly different between years if all treatments were considered (Figs. 2c, d and Table 1).

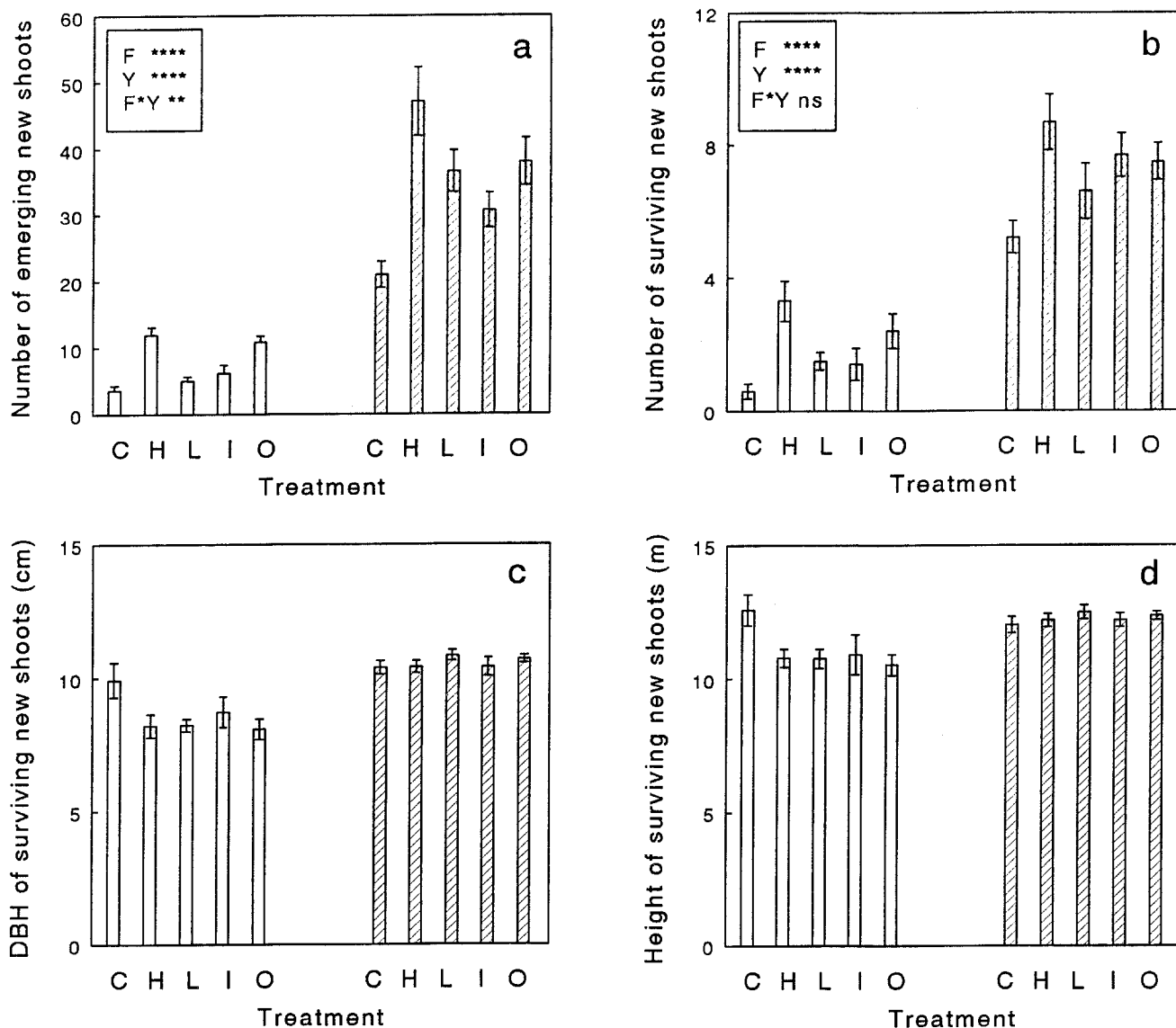


Fig. 2 Mean number and size of new bamboo shoots per plot for different treatments during 1995 (open bars) and 1996 (hatched bars). **(a, b)** number of emerging and surviving new shoots; inset: significance levels of the differences between fertilization treatments

(F, Y), between years (Y) and of the interaction (F×Y); **** $0 < p < 0.0001$; ** $0.001 < p < 0.01$; ns: not significant. **(c, d)**, DBH and height of surviving new shoots, respectively. Data are averages over 10 plots ± S.E.

Effects of fertilizer dosage

The mean number of new shoots emerging and surviving per plot increased significantly with increasing dosage of fertilizer in the spring of both 1995 and 1996 (Table 1, Figs. 2a, b; compare treatments C, L, H). However, DBH and height of surviving new shoots did not depend on fertilizer dosage in either of the two years (Figs. 2c, d). The growth rates of the new shoots were not affected by fertilization either (Figs. 3a, b). New shoots first increased in basal diameter for some weeks and then shifted to rapid height growth. During the fastest elongation of the surviving new shoots (appr. 40 cm height increment per day), many other new shoots died or stagnated. Final survival rates under different treatments were not significantly different from each other; around 20% of the new shoots survived during the springs of both 1995 and 1996 (Figs. 3c, d).

Effects of patchy fertilization

In the spring of 1995, the number of new shoots that emerged in the inner unfertilized parts of the treatment “O” plots was significantly higher than the number that emerged in the equivalent area of the unfertilized control plots (Fig. 4 and Table 2, Ci vs Oi), suggesting that import of resources occurred from the fertilized outer parts to the unfertilized inner parts of the plots. The number of new shoots that emerged in the inner fertilized parts of the “I” plots was significantly lower than the number that emerged in the equivalent area of the treatment “H” plots (Fig. 4 and Table 2, Hi vs li), suggesting that the export of resources to the unfertilized outer parts reduced the number of new shoots in the fertilized inner parts. In the spring of 1996, these differences were also apparent, although they were not significant (Fig. 4 and Table 2). The number of

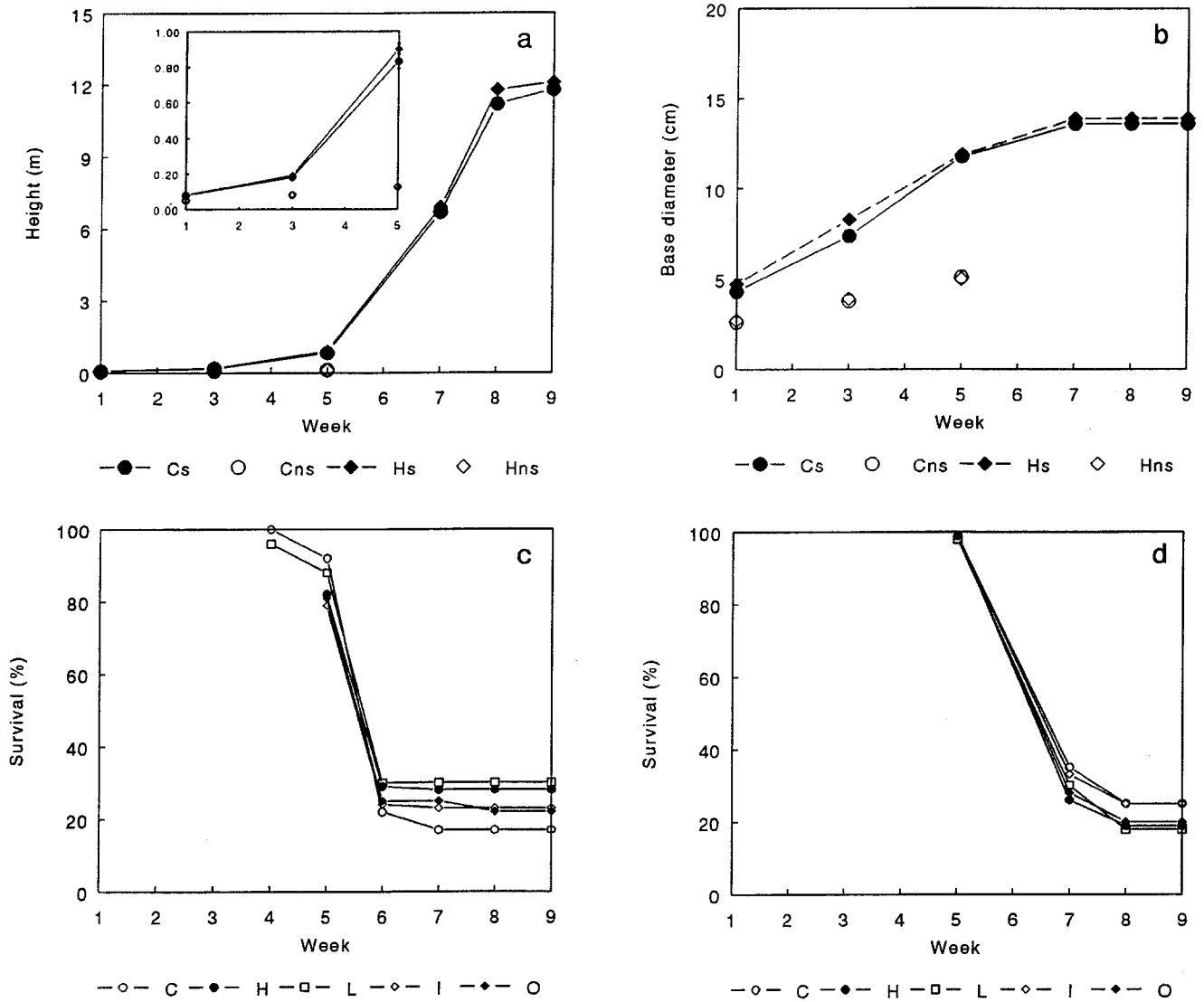


Fig. 3 (a,b) Height and base diameter of new shoots at different censuses from March to May 1996. **a** height (the inset in **a** is an enlarged representation of the pattern during the first five weeks); **b** base diameter; Cs and Cns, surviving and non-surviving new shoots in the unfertilized control plots, respectively; Hs and Hns,

and non-surviving new shoots under fertilized treatment "H", respectively. (c,d) Survival of new shoots from March to May in 1995 (c) and 1996 (d) per treatment; C, H, L, I, O represent treatments as shown in Fig. 1.

new shoots that emerged in the outer unfertilized parts of the "I" plots did not differ significantly from the number that emerged in the equivalent area of the unfertilized control plots, however. Apparently, any import of resources from the fertilized inner parts had been counterbalanced by export to areas beyond the border of the plots. The number of new shoots that emerged in the outer fertilized parts of the "O" plots did not significantly differ from the number that emerged in the equivalent area of the treatment "H" plots, suggesting that any export of resources to the inner, unfertilized part was offset by resources imported from the fertilized buffer zone surrounding the plots of treatment "O" and "H" (Figs. 1, 4).

As expected, the number of new shoots in the inner and outer parts of the plots were similar for the three homogeneous treatments "C", "L", and "H" (Fig. 4). However, this was also the case for the treatments in which fertilizer was heterogeneously applied ("I" and "O"), indicating extensive integration between shoots in unfertilized subplots and those in fertilized subplots.

The total amount of fertilizer applied to the plots (incl. the buffer zone) increased in the order of treatments "I", "L", "O", and "H". Similar increasing trends are seen in the number of emerging and surviving new shoots (Figs. 2a,b). This result indicates that a similar amount of fertilizer induced a similar stimulation of shoot production, irrespective of the method of application (uniform or patchy). Obviously, this applies only to within-plot patchiness; at the larger scale of whole plots plus

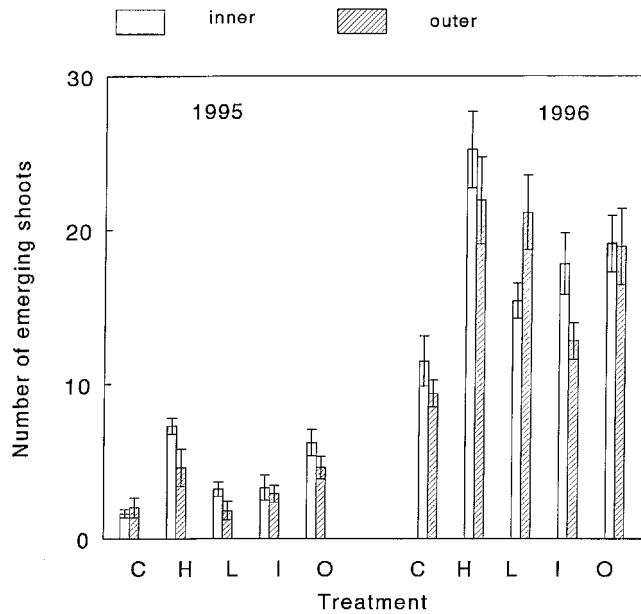


Fig. 4 Mean number of emerging new shoots (\pm S.E.) per inner or outer half of the plots under different treatments in the spring of 1995 and 1996. For each treatment and year, numbers of shoots in the inner and outer halves of the plots did not differ significantly.

border zone, fertilization did increase shoot production compared to the unfertilized surroundings.

Homogeneous versus patchy fertilization of our stands of *P. pubescens* did not lead to differences in growth performance of the shoots in the plots: number, DBH and height of surviving new shoots in the “L”, “I”, and “O” treatments did not differ significantly (Figs. 2b–d; Table 1).

Discussion

Interaction of age structure of adult shoots and nutrient availability

The number of new shoots emerging per plot significantly increased with increasing application of fertilizer in both 1995 and 1996. However, there was a striking difference between years. In 1995 the number increased from 4 ± 1 emerging new shoots per plot in the unfertilized control, to 12 ± 1 shoots per plot in treatment “H”. Yet, this value is still very low in comparison with the value of 21 ± 2 emerging shoots per plot of unfertilized control in 1996. The low production of new shoots in the spring of 1995 and high production in 1996 are in accordance with the two-year cyclic rhythm observed in the study area in recent years (Li et al., 1998 b^[20]). Our results suggest that fertilization will not eliminate these fluctuations.

Recruitment of new shoots is carbohydrate-dependent (Li et al., 1998 d^[22]). The most important limiting factor is the photosynthetic capacity of the stand, which varies with the proportion of new (1st-year) to old (2nd-year) leaves. Because of the two-year life span of *P. pubescens* leaves, the dominance of adult shoots that had emerged in even years (e.g., 1990, 1992 and 1994; see Fig. 5) resulted in a low ratio of 1st:2nd year

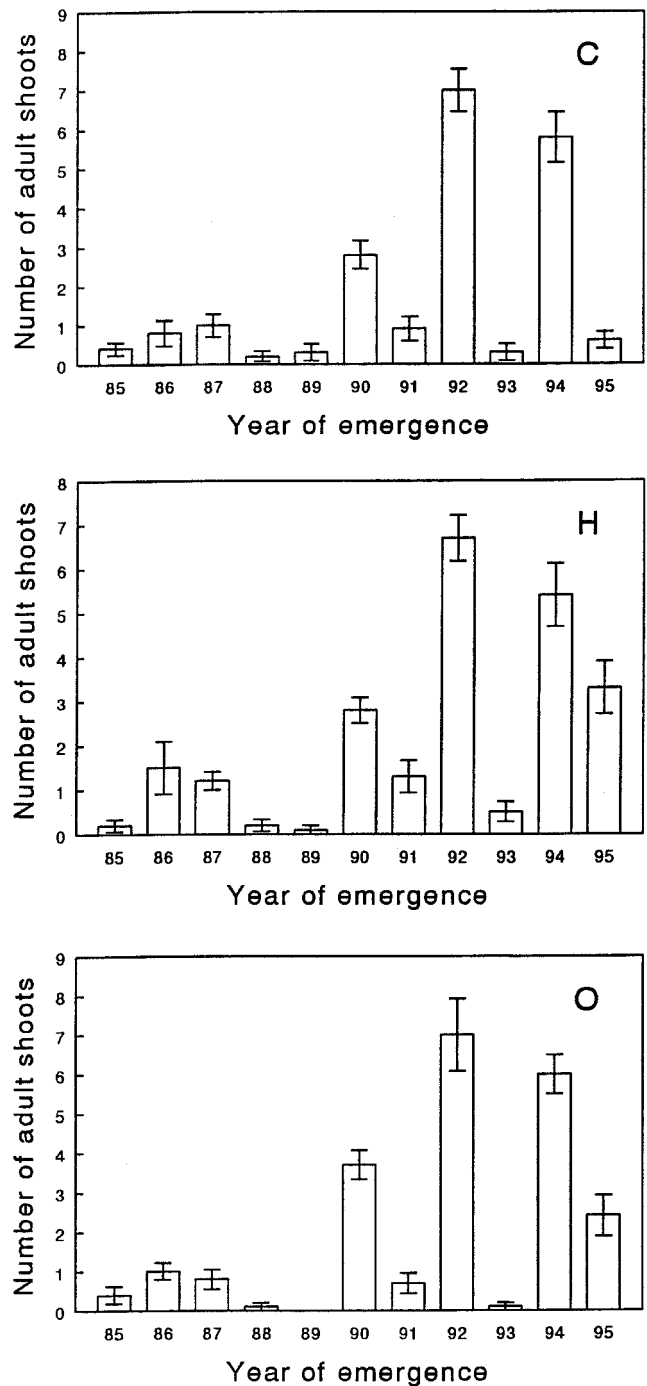


Fig. 5 Mean number of adult shoots (\pm S.E.) at the beginning of March 1996 that had emerged in different years. C, H, and O represent treatments as shown in Fig. 1.

leaves during the growth period of new shoots emerging in 1995, but a high ratio of 1st : 2nd year leaves during the growth period of new shoots emerging in 1996. This explains the differences in the production of new shoots between these years. In addition to these year-to-year differences, there was also an effect of fertilizer. Fertilization lead to higher N and P concentrations in the leaves (N: 26.4 ± 2.0 [fertilized] vs 21.4 ± 2.1 [control] mg g⁻¹ dry matter; P: 1.48 ± 0.08 [fertilized] vs

1.16 ± 0.12 [control] mg g^{-1} dry matter [Li et al., 1998 d^[22]], and therefore its effect on shoot production will probably be due to an increase in the photosynthetic capacity of the leaves.

The rapid responses of this bamboo to fertilization may be due to the following characteristics: 1) the root system in the soil is very dense, amounting to ca. 30 t ha^{-1} root biomass (Li et al., 1998 c^[21]) and 2) the bamboo absorbs and transports nutrients very quickly. When a solution of 20% CuSO_4 is poured into the stumps that remain after the removal of adult shoots, the leaves on the connecting shoots will turn yellow and become withered in 2–3 days. Furthermore, if urea is supplied, the chlorophyll content of the leaves on the fertilized shoots may be 88% higher than that on the unfertilized control shoots in one month (Shi and Bian, 1987^[30]).

Survival and size of new shoots

The survival rates of new shoots were similar for all treatments and all years (approximately 20%). This is in accordance with our previous studies, where the survival rates of new shoots in this bamboo were constant across different sites and different years (Li et al., 1998 a^[19], b^[20]). This result may be due to a within-clone control of new shoot development: proximal new shoots may preempt resources supplied by the nearest connected adult shoots and prevent the growth of new shoots that are positioned more distally on the same rhizome. Consequently, these distal sibling shoots will have a higher chance of dying. In the end, the number of surviving new shoots was in proportion to the number of emerging new shoots, and determined by the number of adult shoots with one-year-old leaves (Li et al., 1998 a^[19], b^[20]) and thus, presumably by the available assimilates (Li et al., 1998 a^[19], b^[20]). In view of the presence of such a mechanism controlling numbers of new shoots, the 80% mortality of new shoots seems to be rather high, but also in other highly integrated clonal plant species, the mortality of subordinate shoots in dense stands has been shown to be quite high (e.g., de Kroon, 1993^[4]; de Kroon and Kalliola, 1995^[5]).

While the number of new shoots was significantly affected, there was no overall effect of fertilization on DBH and height of the new shoots. Yet, if the shoots in unfertilized control plots were excluded, the new shoots surviving under all the fertilized treatments in 1995 were somewhat thinner and shorter than those surviving in 1996 ($p < 0.01$ for both DBH and height), while the new shoots in the control plots of 1995 had the same DBH and height as the shoots of 1996 (Figs. 2c,d). Perhaps, the few adult shoots with one-year-old leaves present in April 1995 were unable to provide sufficient carbohydrates for all surviving shoots to reach "normal" size. In general, it appears that although higher nutrient availability released more buds from dormancy, the shoots developing from these buds ultimately had the same sizes. It thus seems that shoot size was fixed independently of fertilization. The impact on demography of such ontogenetic constraints, i.e., developmental determinations that occur early in the ontogeny and that cannot be modified by conditions experienced later, have enjoyed increasing attention in recent years (Geber et al., 1997 a^[8], b^[9]; Watson, 1984^[37]; Watson et al., 1995^[38]).

Response to spatial heterogeneity of nutrients

In the treatments with patchy fertilization, new bamboo shoots appeared in both the fertilized and the unfertilized plot parts. In the fertilized parts, the number of new shoots was less than in the equivalent areas of the homogeneously fertilized "H" plots, while in the unfertilized parts the number of new shoots was higher than in the equivalent areas of the unfertilized control "C" plots. This indicates transport of nutrients from the fertilized parts to the unfertilized parts. While such transport may have taken place via roots crossing the border between both plot parts, the restricted length and predominantly vertical direction of growth of these roots (Li et al., 1998 c^[21]) suggest that this can account for only a small part of the transport. Apparently, translocation of resources occurred mainly through the rhizome system.

To our knowledge, our study is the first to examine the effects of patchy fertilization on a canopy-forming clonal plant. Our results suggest that the performance of entire clones of *P. pubescens* in a patchy habitat did not exceed the performance in a uniform habitat with the same amount of resources, in contrast to the results with *Glechoma hederacea* of Birch and Hutchings (1994^[3]). The explanation may be that the benefits to clone parts in unfertilized patches were offset by the costs to the clone parts in the fertilized patches. Moreover, Birch and Hutchings (1994^[3]) started with small clone fragments that grew out into unoccupied territory. In their patchy treatment, the plants reached the high-nutrient patch early in their development, specialized on the local conditions by the production of a large root mass in this patch, and thus were able to extract a larger proportion of the available nutrients earlier in their growing period than was possible in the homogeneous treatment. This speeded up the production of ramets (and thus of photosynthesizing leaf area) of clone parts distal to the high-nutrient patch, which finally led to the better performance of the plants in the patchy treatment. The lack of additional benefits of patchy fertilization in our experiment may be related to the fact that the plants already covered the whole area before the application, which allowed rapid integration in terms of nutrients and carbohydrates over the whole area, while the production of new shoots is a much more time-consuming process.

In *P. pubescens*, integration evened out the (within-plot) effects of the patchiness that were imposed, resulting in a similar number of new shoots emerging in exporting and importing parts of the clone. Hutchings and Price (1993^[14], p. 95) questioned whether "physiological integration between the ramets of clonal herbs evens out the effect of variation in environmental quality". In this context, morphological responses (e.g., biomass allocation to roots, shoots, and petioles) should be clearly separated from effects on overall biomass production. Clonal plants with strong physiological integration indeed show highly local morphological responses to patch environment in a heterogeneous habitat (Hutchings and Price, 1993^[14]; Stuefer et al., 1996^[33], 1994^[34]). Hutchings and Price also argued, however, that "supplying resources to another part of the clone's structure would retard growth and exploitation of the resources in the better patch" (Hutchings and Price, 1993^[14], p. 103). This will especially be the case if the ramets in the better patch encounter strong competition for light from other plants in that patch. In the *P. pubescens* groves, however, the canopy

structure (consisting of *P. pubescens* itself) is unlikely to show a rapid increase in LAI and an increased competition for light in response to fertilization. In fact, if evening out of the patchily distributed resources would not occur, this would eventually result in a higher shoot density in the high-nutrient patches (if fertilization would continue to result in higher recruitment rates as in our "H" treatment), and thus more competition for light between the ramets than in the case of extensive physiological integration. So, in view of the high LAI values generally found in groves of *P. pubescens* (Fliervoet et al., 1989^[7]; Li et al., 1998 c^[21]), in the long run, we would expect that the evening out of a patchy availability of nutrients by physiological integration would enhance the productivity of the stand. This reinforces the conclusion of Dong (1995^[6]) that the solution to the controversy raised by Hutchings and Price (1993^[14]), whether integration would be beneficial if it leads to an evening out or an enhancement of local responses, may be strongly species- and habitat-dependent.

Acknowledgements

We would like to thank Drs. M. Dong, J. A. J. Faber, H. Huber, J. F. Stuefer, J. H. Willems, and R. J. Zagt for their valuable suggestions and/or critical reading of the manuscript. This study is supported by grant W86-117 of the Netherlands Foundation for the Advancement of Tropical Research to Prof. Werger and grant 39330050 of the National Natural Science Foundation of China for Plant Population Ecology Research to Prof. Zhong.

References

- 1 Alpert, P. and Stuefer, J. F. (1997) Division of labour in clonal plants. In *The ecology and evolution of clonal plants* (de Kroon, H. and van Groenendael, J., eds.), Leiden: Backhuys Publishers, pp. 137–154.
- 2 Bamboo Research Institute of Nanjing Forestry University (1974) *Cultivation of bamboo groves*. Beijing: Agriculture Press, p. 278.
- 3 Birch, C. P. D. and Hutchings, M. J. (1994) Exploitation of patchily distributed soil resources by the clonal herb *Glechoma hederacea*. *J. Ecol.* 82, 653–664.
- 4 de Kroon, H. (1993) Competition between shoots in stands of clonal plants. *Plant Species Biol.* 8, 85–94.
- 5 de Kroon, H. and Kalliola, R. (1995) Shoot dynamics of the giant grass *Gynerium sagittatum* in Peruvian Amazon floodplains, a clonal plant that does show self-thinning. *Oecologia* 101, 124–131.
- 6 Dong, M. (1995) Morphological responses to local light conditions in clonal herbs from contrasting habitats, and their modification due to physiological integration. *Oecologia* 101, 282–288.
- 7 Fliervoet, L. M., Zhong, Z. C., Liu, Y. C., Miao, S. L., Dong, M., and Werger, M. J. A. (1989) Diversity and above-ground structure of the understorey of *Phyllostachys pubescens* groves on Mount Jinyun, Sichuan, China. *Flora* 182, 203–219.
- 8 Geber, M. A., de Kroon, H., and Watson, M. A. (1997 a) Organ preformation in mayapple as a mechanism for historical effects on demography. *J. Ecol.* 85, 211–223.
- 9 Geber, M. A., Watson, M. A., and de Kroon, H. (1997 b) Organ preformation, development, and resource allocation in perennials. In *Plant resource allocation* (Bazzaz, F. A. and Grace, J., eds.), New York: Academic Press, pp. 113–141.
- 10 Hirose, T. and Werger, M. J. A. (1987) Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* 72, 520–526.
- 11 Hsiung, W. Y., Xiao, J. H., and Lou, Y. P. (1990) Development of rhizome-culm systems in a newly established stand of *Phyllostachys praecox*. *Bamboo J. (Japan)* 8, 64–68.
- 12 Huang, Q. M. and Yang, D. D. (1989) Research on photosynthesis of bamboo. *Bamboo Res. (China)* 8 (2), 8–18.
- 13 Hutchings, M. J. (1979) Weight-density relationships in ramet populations of clonal perennial herbs, with special reference to the $-3/2$ power law. *J. Ecol.* 67, 21–33.
- 14 Hutchings, M. J. and Price, E. A. C. (1993) Does physiological integration enable clonal plants to integrate the effects of environmental heterogeneity? *Plant Species Biol.* 8, 95–105.
- 15 Hutchings, M. J. and Wijesinghe, D. K. (1997) Patchy habitats, division of labour and growth dividends in clonal plants. *Trends Ecol. Evol.* 12, 390–394.
- 16 Isagi, Y., Kawahara, T., Kamo, K., and Ito, H. (1997) Net production and carbon cycling in a bamboo *Phyllostachys pubescens* stand. *Plant Ecol.* 130, 41–52.
- 17 Janzen, D. H. (1976) Why bamboos wait so long to flower. *Annu. Rev. Ecol. Syst.* 7, 347–391.
- 18 Jónsdóttir, I. S. and Watson, M. A. (1997) Extensive physiological integration: An adaptive trait in resource-poor environments? In *The ecology and evolution of clonal plants* (de Kroon, H. and van Groenendael, J., eds.), Leiden: Backhuys Publishers, pp. 109–136.
- 19 Li, R., During, H. J., Werger, M. J. A., and Zhong, Z. C. (1998 a) Positioning of new shoots relative to adult shoots in groves of giant bamboo *Phyllostachys pubescens*. *Flora* 193, 315–321.
- 20 Li, R., Werger, M. J. A., During, H. J., and Zhong, Z. C. (1998 b) Biennial variation in production of new shoots in groves of the giant bamboo *Phyllostachys pubescens* in Sichuan, China. *Plant Ecol.* 135, 103–112.
- 21 Li, R., Werger, M. J. A., During, H. J., and Zhong, Z. C. (1998 c) Biomass distribution in a grove of the giant bamboo *Phyllostachys pubescens* in Chongqing, China. *Flora* 194, 89–96.
- 22 Li, R., Werger, M. J. A., During, H. J., and Zhong, Z. C. (1998 d) Carbon and nutrient dynamics in relation to growth rhythm in the giant bamboo *Phyllostachys pubescens*. *Plant and Soil* 201, 113–123.
- 23 Liao, G. L. (1990) On the flowering and regeneration of *Phyllostachys pubescens*. *Bamboo J. (Japan)* 8, 21–23.
- 24 Liu, Y. C., Fliervoet, L. M., Zhong, Z. C., and Werger, M. J. A. (1988) Stand structure of giant bamboo (*Phyllostachys pubescens*) groves in Sichuan, China. In *Vegetation structure in relation to carbon and nutrient economy: production, decomposition and atmospheric interception* (Verhoeven, J. T. A., Heil, G. W., and Werger, M. J. A., eds.), The Hague: SPB Academic Publishing, pp. 37–43.
- 25 MacClure, F. A. (1966) *The bamboos: a fresh perspective*. Cambridge, Massachusetts: Harvard University Press, p. 347.
- 26 Marshall, C. (1990) Source-sink relations of interconnected ramets. In *Clonal growth in plants: regulation and function* (van Groenendael, J. and de Kroon, H., eds.), The Hague: SPB Academic Publishing, pp. 23–41.
- 27 Mooney, H. A. (1986) Photosynthesis. In *Plant ecology* (Crawley, M. J., ed.), Oxford: Blackwell Scientific Publications, pp. 345–374.
- 28 Numata, M. (1979) Structure and succession of bamboo vegetation. In *Ecology of grasslands and bambuolands in the world* (Numata, M., ed.), The Hague: Dr. W. Junk Publishers, pp. 237–258.
- 29 Pitelka, L. F. and Ashmun, J. W. (1985) Physiology and integration of ramets in clonal plants. In *Population biology and evolution of clonal organisms* (Jackson, J. B. C., Buss, L. W., and Cook, R. E., eds.), New Haven: Yale University Press, pp. 399–437.
- 30 Shi, Q. T. and Bian, Y. R. (1987) Study on the application of chemical fertilizers in bamboo stump. *J. Bamboo Res. (in Chinese)* 6, 24–34.
- 31 Sokal, R. R. and Rohlf, F. J. (1995) *Biometry*, 3d ed. New York: W. H. Freeman and Company, p. 887.
- 32 StatSoft Inc. (1993) *Statistica for Windows*. Tulsa, Oklahoma, USA: Release 4.5.
- 33 Stuefer, J. F., de Kroon, H., and During, H. J. (1996) Exploitation of environmental heterogeneity by spatial division of labour in a clonal plant. *Funct. Ecol.* 10, 328–334.

- ³⁴ Stuefer, J. F., During, H. J., and de Kroon, H. (1994) High benefits of clonal integration in two stoloniferous species, in response to heterogeneous light environments. *J. Ecol.* 82, 511–518.
- ³⁵ Suzuki, J. and Hutchings, M. J. (1997) Interactions between shoots in clonal plants and the effects of stored resources on the structure of shoot populations. In *The ecology and evolution of clonal plants* (de Kroon, H. and van Groenendael, J., eds.), Leiden: Backhuys Publishers, pp. 311–329.
- ³⁶ Ueda, K. (1960) Studies on the physiology of bamboo, with reference to practical application. *Bulletin of the Kyoto University of Forestry* 30, 1–169.
- ³⁷ Watson, M. A. (1984) Developmental constraints: effect on population growth and patterns of resource allocation in a clonal plant. *Am. Nat.* 123, 411–426.
- ³⁸ Watson, M. A., Geber, M. A., and Jones, C. S. (1995) Ontogenetic contingency and the expression of plant plasticity. *Trends Ecol. Evol.* 10, 474–475.
- ³⁹ Wu, B. S. (1984) A preliminary analysis of the relationship between the underground structure of a *Phyllostachys pubescens* forest and its yield. *J. Bamboo Res.* (in Chinese) 3, 49–58.
- ⁴⁰ Zhou, J. Y., Hu, C. Z., and Yan, L. P. (1985) Investigations on the rhizomes of bamboo groves for food consumption. *J. Bamboo Res.* (in Chinese) 4, 57–64.

M. J. A. Werger

Department of Plant Ecology and Evolutionary Biology
University of Utrecht
P.O. Box 800.84
3508 TB Utrecht
The Netherlands

E-mail: m.j.a.werger@bio.uu.nl

Section Editor: R. Aerts