中国亚热带高大竹类植物毛竹
竹笋克隆生长的密度调节

李　睿　钟章成

（西南师范大学生命科学系，重庆　630715）

M. J. A. 维尔格

（荷兰乌德勒支大学植物生态学与进化生物学系）

摘　要　对许多多年生克隆植物来说，大量的研究表明：当光是限制因子时，随着立地密度的不断增加，克隆分株的出生率逐渐减小、死亡率逐渐增加。本文观测了乔木状高大竹类植物毛竹竹笋的出生与存活过程，结果表明：竹笋的出生率，即每样方的出笋数，明显地随着成竹立竹度的增加而增加。更确切地说，竹笋的数量，不管是出笋数还是活笋数，都明显地随着带新叶（1龄叶）的成竹立竹度的增加而增加，而与带老叶（2龄叶）的成竹立竹度相关性不显著。并且竹笋的死亡率是非密度制约的。这可能是由于对毛竹来说，其立地总是比较开敞，而且，其竹笋的生长在很大程度上是不直接需光的。

关键词　克隆生长　密度制约　叶龄　死亡率　出生率　毛竹

DENSITY REGULATION OF THE CLONAL GROWTH OF NEW SHOOTS IN THE GIANT BAMBOO *PHYLLOSTACHYS PUBESCENS* IN SUBTROPICAL CHINA[*]

Li Rui and Zhong Zhangcheng

（*Department of Life Science*，*Southwest China Normal University*，Chongqing 630715 China）

M. J. A. Werger

（ *Department of Plant Ecology and Evolutionary Biology*，*University of Utrecht*，

P. O. Box 800. 84，3508 TB Utrecht，The Netherlands）

Abstract　It has been shown that in many clonal perennials，when light is limiting，shoot natality decreases and shoot mortality increases with increasing stand density. In this paper，emergence and

---

survival of new shoots in a giant bamboo *Phyllostachys pubescens*, were observed in 25 permanent plots, each 6 m × 6 m, over a period of eight censuses at weekly intervals. Our results show that in this bamboo, shoot natality (the number of newly emerged shoots per plot) significantly increased with increasing density of adult shoots. More precisely, the number of newly emerged and/or surviving shoots, significantly increased with increasing density of adult shoots carrying new leaves, but not with that of those carrying old leaves. Furthermore, shoot mortality was density independent. This may be due to the fact that the stands where *P. pubescens* exists always remain relatively open, and the growth of the new shoots is not directly light-dependent.

Key words   Clonal growth, Density dependence, Leaf age, Mortality, Natality, *P. pubescens*

Clonal perennial plants are dominant components in many plant communities and some form near-monocultures. Their shoots may be physically connected by means of rhizomes or stolons (Hutchings *et al.*, 1976; Maddox *et al.*, 1989; van der Toorn *et al.*, 1982), allowing resources such as carbohydrates, nutrients and water to be translocated between connected shoots (Marshall, 1990; Pitelka *et al.*, 1985). A number of studies have shown that as a result of physiological integration, shoot natality decreases whereas shoot mortality increases in stands of increasing density (Bradbury, 1981; Briske *et al.*, 1989; de Kroon *et al.*, 1991; Dickerman *et al.*, 1985; Harnett *et al.*, 1985; Hutchings *et al.*, 1976; Lapham *et al.*, 1987; Liddle *et al.*, 1982). Even self-thinning has been reported in a clonal species (de Kroon *et al.*, 1995).

In high density stands density dependence results largely from shoot density being limited by the environmental carrying capacity as mainly determined by light levels in the stands (de Kroon *et al.*, 1995; de Kroon *et al.*, 1991). In relatively open stands of clonal plants, or where new shoots do not directly compete for light, we may expect that natality will increase with increasing parent shoot density, because more parent shoots can allocate more resources to daughter shoots.

On the other hand, during the growth of new bamboo shoots of *Phyllostachys* resources are apically translocated from parent shoots to daughter shoots through rhizomes (Bamboo Research Institute of Nanjing Forestry University, 1974). In respect to the absorption of resources, daughter shoots nearest to the parent shoots have precedence over the others on the rhizome. Thus the positions of daughter shoots away from a parent shoot along a rhizome have great influences on their growth potential and survival possibility. We may expect shoot survival (or death) rate will not vary with varying density of parent shoots, *i.e.* shoot mortality will be density independent.

Besides, it is well known that the age structure plays an important role in the dynamics of populations (Harper, 1977). Yet, little is known about age of clonal perennials because it is very difficult to determine.

In this paper we present results of a field investigation on the recruitment of new bamboo shoots in a population of *Phyllostachys pubescens* Mazel. It is a giant bamboo species native to subtropical China, where it is widely distributed and cultivated with care. Every year 7~10 years old shoots are selectively harvested for timber use. Therefore, the bamboo groves always remain rela-

tively open and leave lots of gaps to be filled by new shoots from year to year.

New shoots of *Phyllostachys* are tightly wrapped with brown sheaths until reaching the canopy of the stands. Then they develop their first branch. It has been found that for at least a dozen days, the new shoots grown in a darkroom and covered by black cloth grew as well as those under normal conditions (Ueda, 1960). This indicates that the growth of the new shoots mainly depends upon the resources stored in the parents (including rhizomes).

In southern China, year of emergence of every surviving new shoot is marked permanently with colour paint on its stem around June of every year. So we can relate the age structure of parent shoots to the potential of regeneration.

Here we want to test the above mentioned hypothesis of positively density-dependent natality and density-independent mortality in *P. pubescens*.

1　MATERIALS AND METHODS

1.1　The species and study area

P. pubescens is a monopodial bamboo species and its shoots are widely spaced inside the stands. Height of mature shoots often reaches over 10m and sometimes up to 20m, and their diameters at breast height (DBH) range from 6~16cm, but there is no clear shoot size hierarchy in stands of this species. No signs of decay of rhizome connections between living shoots were observed during investigation.

In this bamboo, leaves have life span of two years, except those on the first year shoots whose life span is one year. Two years old leaves and leaves on the first year shoots are dropped in April, during the emergence and elongation of new shoots (Bamboo Research Institute of Nanjing Forestry University, 1974). Thus, in April four types of shoots can be recognized: 1) newly emerged shoots which have no leaves; 2) one year old shoots that have fully vertically grown and are dropping their leaves formed during the first year (henceforward called "first year shoots"); 3) mature shoots which are just dropping their two years old leaves (henceforward called "adult shoots with old leaves"); 4) mature shoots with leaves formed the year before and kept on the shoots for another year (henceforward called "adult shoots with new leaves").

New shoots emerge from buds on rhizomes which are belowground at a depth of about 15~40cm. The number of new shoots formed on a rhizome seems to decrease markedly with the rhizome aging (Ueda, 1960). Lateral buds are activated every summer and new shoots then emerge aboveground every following spring (March, April). At about the end of April, a great number of new shoots showing symptoms of dying (*i.e.* having no guttation on the tips of sheaths covering the emerging shoots, loosening of the sheaths, and cessation of height growth) will be harvested for consumption. The shoot population structure thus mainly depends on the births, deaths and harvests of new shoots, and on the harvests of adult shoots.

Once the new shoots reach the canopy, they begin to shed their sheaths and develop branches and leaves. Normally all tall shoots keep alive for $7 \sim 10$ years after emergence, and then they were harvested for timber use. Therefore, it also is of practical importance to understand the regeneration pattern of this bamboo species.

The bamboo stands were situated in the Nature Reserve of Jinyun Mountain (29°50′N, 106°26′E), about 40km north of the city of Chongqing, Sichuan province, China. They cover some 30 hectares. We learned from the local people that it had a stable history of more than 40 years. This area was exposed to the East Asian monsoon. From 1976 to 1993, average temperature in the coldest month was between 5.2℃ and 9.4℃, in the hottest month between 24.9℃ and 30.4℃, and annual average temperature was between 17.6℃ and 18.7℃. The average annual precipitation was between 913.1mm and 1514.0 mm (according to data from Beibei Weather Station, alt. 215m, at the foot of Jinyun Mountain). The study sites were located at the middle of a slope of about 15 degrees, facing northeast, at about 800m above sea level.

1.2 Methods

25 permanent plots, each 6m × 6m, were randomly placed in the centre of the bamboo forest. In March 1994, before emergence of new shoots, the parent shoots in each plot were counted, and the age of each parent shoot was ascertained and recorded. From the end of March 1994, new shoots began to emerge. We made the first census on April 1, and successively censuses at weekly intervals until May 20th, 1994, when all surviving new shoots reached the canopy and began to branch. During each census, newly sprouted shoots were marked and numbered by means of a small bamboo-stick stuck into the soil next to each new shoot. Base girths and heights were measured for each new shoot at each census. At the end of April 1994, when new shoots going to surviving appeared obviously different from those doing to be harvested and going to die, 40 rhizomes outside the permanent plots, were randomly excavated with care to observe the relationship between the sequence of these shoots on their rhizomes and the shoot survival possibility.

Relations between the number of emerging or surviving new shoots per plot and the number of parent shoots with new or old leaves per plot were investigated using regression analysis. Oneway ANOVA and LSD technique (Steel and Toorie, 1960) were used to test the significance of differences in size (in terms of both base girths and heights) between new shoots with different fates in each census, and the significance of differences in size between censuses for each group of new shoots with the same fate.

2 RESULTS

2.1 Emergence and survival

New bamboo shoots emerged aboveground from about the end of March to the end of

April 1994. Thereafter no emergences were observed. There were altogether 316 new shoots in the 25 permanent plots, and the number of new shoots in a plot ranged from 6 to 28. Losses of new shoots resulted from deaths and harvests. There were no deaths during the first four censuses. 135 (43%) new shoots died during the fourth to seventh census. 112 (35%) new shoots which showed symptoms to die, were harvested for consumption during the fifth to the seventh census. 69 (22%) new shoots survived (Fig. 1).

Based on the time of emergence aboveground, age-specific survivorship curves were drawn for certain cohorts in the population (Fig. 2). Death occurred mainly during the period of 4~7 census, irrespective of the age of new shoots.
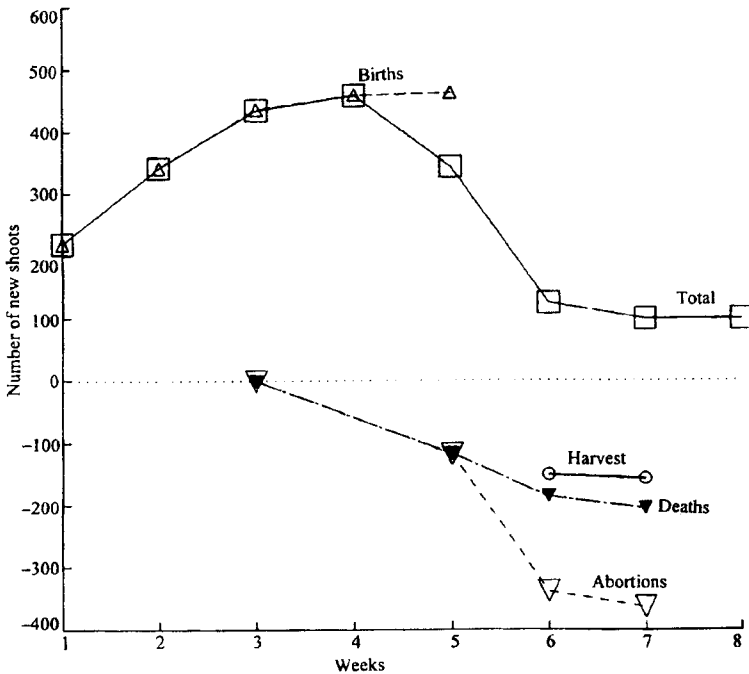

Fig. 1   Number of new shoots in 25 permanent plots in the
Phyllostachys pubescens stands
Births, cumulative number of emerging shoots; Deaths, cumulative number of died
shoots; Harvest, cumulative number of harvested shoots; Total, number of surviving
shoots ; Abortions, number of died+harvested shoots

On 40 excavated rhizomes, there were altogether 118 emerged new shoots, the number of shoots on a rhizome ranged from 0 to 5. All 28 shoots appeared going to survive were the first 1~2 ones on the rhizomes. The other 90 shoots appeared going to be harvested or going
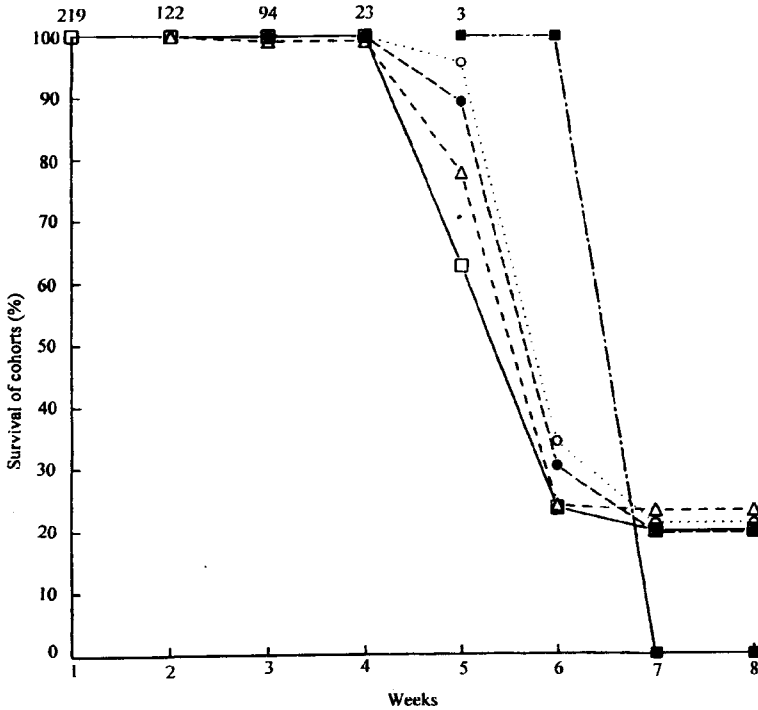
Fig. 2 Survival of cohorts of new shoots of *Phyllostachys pubescens*.
The initial number of new shoots in each cohort is indicated

to die. Of them, 79 (88%) were the 2~5th new shoots on the rhizomes, 11 (12%) were
the first ones.

2.2 Density of shoots

The number of newly emerged shoots per plot (natality) and the number of surviving
new shoots per plot were positively correlated with the number of adult shoots per plot ($r=$
$0.40; p<0.05$ and $r=0.44; p<0.05$, respectively). More precisely, natality was positively
correlated with the number of adult shoots carrying new leaves ($r=0.53; p<0.01$), but not
correlated with that of those carrying old leaves ($r=-0.27; p>0.05$); and the number of
surviving new shoots per plot also was positively correlated to the number of adult shoots
carrying new leaves ($r=0.52; p<0.01$), but not correlated to the number of adult shoot
carrying old leaves ($r=-0.09; p>0.05$).

The ratios of the total number of newly emerged shoots and surviving new shoots to the
total number of adult shoots, which are the per capita rates of birth and survival, were 1.32
and 0.29 respectively. The ratios were 2.41 and 0.53 respectively, as they were with respect
to the adult shoots carrying new leaves. Overall density measures of adult shoots masked the
differences in resources supplying capacity to new shoots between adults carrying new and

old leaves. Besides, the number of new shoots aborted, both died and harvested per plot, were proportional to the number of emerged new shoots (Fig. 3), suggesting that mortality rates were relatively constant across all plots independent of density.

2.3 Differential size growth

Size (in terms of base girth and height) of new shoots with different fates differed significantly at each census (Table 1). At the beginning, mean base girth of new shoots that ultimately survived was about 1.1 and 1.8 fold larger than that of those to be harvested and to die respectively, and the corresponding differences in mean heights were 1.3 and 2.1 fold. Up to the fourth census, after which synchronized massive death of smaller and shorter new shoots occured the larger and taller new shoots vigorously elongated, the size differences between new shoots that ultimately survived and the new shoots that were to be harvested or were to die increased up to 1.6 and 4.4 fold in terms of base girths, and 3.9 and 19.7 fold in terms of heights. Thereafter, there were no great changes in base girths for all new shoots. The heights of new shoots going to die stayed more or less stable, heights of new shoots going to be harvested grew relatively slowly, while the new shoots to survive elongated very fast before entering the top of canopy; at the sixth census the height differences between new shoots going to survive and new shoots going to be harvested or going to die had augmented up to 13.8 and 111.4 fold, respectively. At the seventh census, only the new shoots surviving remained in the plots. These data show that larger and taller new shoots grow disproportionably faster than smaller and shorter ones. A large number of smaller, shorter new shoots die during the period of vigorous growth of the larger and taller ones.
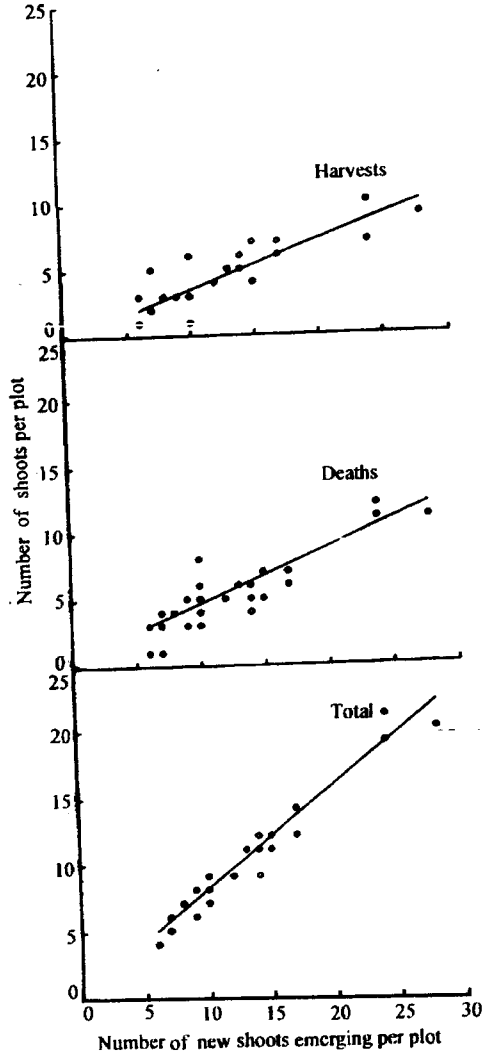

Fig. 3　The relationship between the number of new shoots lost (y, both died and harvested) per plot and the number of new shoots emerging per plot (x)

Regression lines are all highly significant: Deaths: $y = 0.03 + 0.42x, t = 8.90, df = 23, t > t_{0.01}$; Harvests: $y = 0.04 + 0.35x, t = 7.44, df = 23, t > t_{0.01}$; Total lost: $y = 0.07 + 0.78x, t = 21.01, df = 23, t > t_{0.01}$

Table 1　Mean base girths and mean heights of new shoots that are going to die (deaths), will be harvested (harvests) and survive (survival) measured at each census for *Phyllostachys pubescens*. S. E. are given in parentheses and number of observations are given in square brackets. Differences between new shoot groups at each census and between censuses within each new shoot group were tested for significance separately; values with the same letter are not significantly different at $p = 0.05$

	Deaths (cm)			Harvests (cm)			Survival (cm)		
Base girth									
wk. 1	6.9	(2.8) a	[113]	10.3	(3.9) b	[61]	12.2	(4.8) c	[45]
wk. 2	8.7	(3.4) d	[159]	15.2	(5.3) e	[108]	20.2	(5.5) f	[74]
wk. 3	10.0	(4.2) g	[192]	25.1	(7.7) h	[150]	39.8	(8.6) i	[93]
wk. 4	10.4	(4.6) g	[203]	27.5	(8.4) j	[156]	45.1	(8.4) k	[98]
wk. 5	12.4	(5.4) l	[87]	28.2	(8.4) j	[157]	47.7	(6.3) m	[98]
wk. 6	12.6	(5.5) l	[19]	29.3	(9.1) j	[6]	47.7	(6.3) m	[98]
wk. 7	none			none			47.7	(6.3) m	[98]
wk. 8	none			none			47.7	(6.3) m	[98]
Height									
wk. 1	2.4	(1.3) a	[113]	3.5	(1.7) b	[61]	4.9	(2.6) c	[45]
wk. 2	3.3	(1.7) d	[159]	6.9	(3.1) b	[108]	9.7	(3.4) c	[74]
wk. 3	4.4	(2.7) e	[192]	17.7	(8.6) f	[150]	41.4	(17.8) g	[93]
wk. 4	4.8	(3.2) e	[203]	22.7	(12.3) h	[156]	91.7	(45.0) i	[98]
wk. 5	6.2	(4.2) j	[87]	26.7	(17.4) k	[157]	286.5	(111.3) l	[98]
wk. 6	6.2	(4.0) j	[19]	59.5	(41.0) m	[6]	675.5	(166.7) n	[98]
wk. 7	none			none			1035.6	(165.0) o	[98]
wk. 8	none			none			1303.4	(147.3) p	[98]

3　DISCUSSION

3. 1　Density dependent effects

Our results show that natality of new bamboo shoots was positively density dependent on adult shoots. More particularly, the number of new shoots was positively density dependent on adults carrying new leaves, not on those carrying old leaves. In this bamboo, the photosynthetic capacity of new leaves has been reported to be able to exceed that of old leaves by 3. 3 times (Huang Qiming *et al.* , 1989). Such differences in photosynthetic capacity between new and old leaves also found in other plant species (Mooney *et al.* , 1983). These togather suggest that the amount of assimilates stored in parents (adult shoots and rhizomes) controls the number of new shoots that are produced and establish themselves successfully. Thus, physiological integration among shoots seems to at a large extent regulate the recruitment of new shoots.

Ye Zhiyun (1988) also found that in *P. pubescence*, number of new shoots surviving per plot was positively density dependent on adult shoots. This contrasts with many studies on other clonal plants. Their shoot production was found to be negatively correlated with the density of stand (Briske *et al.* , 1989; de Kroon *et al.* , 1991; de Kroon *et al.* , 1995; Harnett *et al.* , 1985; Lapham *et al.* , 1987). The elongating new bamboo shoots do not require light until reaching the canopy, where upon they shed their sheaths and develop branches and

leaves. Until then they seem to completely live on the resources stored in the parents. So, the more adult shoots, the more resources they can provide, and the more new shoots can be produced. This explains the positive density dependence in our stands. From model studies on other clonal plants we know, however, that there is an optimal stand density for maximum productivity of the stands (Schieving *et al.*, 1992). It is reasonable to expect the production of new shoots also to decline beyond maximum point.

Knowledge on the pattern of density dependent effects is important for understanding the mechanisms controlling the reported usual year to year fluctuation in the production of new bamboo shoots (Bamboo Research Institute of Nanjing Forestry University, 1974; Ueda, 1960). In "good" years a larger amount of new shoots are produced than in "poor" years. This may be largely explained by the fact that the number of adults carrying new and old leaves in the stands were not equal. We showed that the adults carrying new leaves play a significantly more important role than those carrying old leaves as regards new shoot production. Since the new shoots drop their leaves at the end of the first year and then start to develop leaves that persist for two years, they join the group of adults with new leaves that gave rise to their emergence and thus contribute to the existing rhythm. The inequality in numbers of adults with new or old leaves can be due to the careless removal of adults in a certain year or due to the occasional occurrence of other limiting factors, such as severe drought and serious pest. Once such a population structure is formed, it will inevitably result in a fluctuation in the production of new shoots from year to year, until the population structure of the adult shoots is readjusted to equal numbers of adults carrying new and old leaves.

3.2 Size differentiation

Larger and taller new shoots, which were the nearest to their parents on the rhizomes, obtained a disproportional share of the resources over smaller and shorter new shoots, which were farther away from their parents. Smaller and shorter new shoots had a significantly higher mortality risk. And shoot mortality was density independent. Survivorship increasing with size of the young shoots has also been reported in a clonal palm species (De Steven, 1989). The smaller and shorter *Phyllostachys* shoots were usually harvested, and there are strong reasons to assume that most of them would inevitably die even if they were not harvested. Theoretically, removal of these smaller new shoots may somewhat reduce the cost of resources. From a management point of view, harvesting those stagnated new shoots for consumption is one of the most effective ways for a maximum utilization of bamboo shoot resources.

REFERENCES

Bamboo Research Institute of Nanjing Forestry University, 1974: *Cultivation of bamboo groves*. Agriculture Press, Beijing, 1～201.

Bradbury,I. K. ,1981:Dynamics,structure and performances of shoot populations of *Solidago canadensis* L. in abandoned pastures. *Oecologia* **48**:271~276.

Briske,D. D. ,Butler,J. L. ,1989:Density dependent regulation of ramet populations within the bunchgrass *Schizachyrium scoparrium*:Interclonal versus intraclonal interference. *Journal of Ecology* **77**:963~974.

De Kroon,H. ,Kalliola,R. ,1995:Shoot dynamics of the giant grass *Gynerium sagittatum* in Peruvian Amazon floodplain; a clonal plant that does show self-thinning. *Oecologia* **101**:124~131.

De Kroon,H. ,Kwant,R. ,1991:Density-dependent growth responses in two clonal herbs:regulation of shoot density. *Oecologia* **86**:298~304.

De Steven,D. ,1989:Genet and ramet demography of Oenocarpus mapora ssp. mapora, a clonal palm of Panamanian tropical moist forest. *Journal of Ecology* **77**:579~596.

Dickerman,J. A. ,Wetzel,R. G. 1985:Clonal growth in *Typha latifolia*:population dynamics and demography of the ramets. *Journal of Ecology* **73**:535~552.

Harper,J. L. ,1977:*Population biology of plants*. Academic Press,London and New York.

Harnett,D. C. ,Bazzaz,F. A. 1985:The regulation of leaf,ramet and genet densities in experimental populations of rhizomatous perennial *Solidago canadensis. Journal of Ecology.* **73**:429~443.

Huang Qiming,Yang Didie,Gao Aixin,1989:The research on photosynthesis of bamboo. Bamboo Research (China) **8** (2) 8~18.

Hutchings,M. J. ,Barkham,J. P. ,1976:An investigation of shoot interactions in *Mercurialis perennis* L. ,a rhizomatous perennial herb. *Journal of Ecology* **64**:723~743.

Lapham,J. ,Drennan,D. S. H. ,1987:Intraspecific regulation of a population of clonal herbs,*Cyperus esculentus, Journal of Applied Ecology* **24**:1011~1024.

Liddle,M. J. ,Budd,C. S. J. ,Hutchings,M. J. ,1982: Population dynamics and neighbourhood effects in establishing swards of *Festuca rubra. Oikos* **38**:52~59.

Maddox,G. D. ,Cook,R. E. ,1989:Clonal structure in four *Solidago altissima* (Asteraceae) populations:rhizome connections within genotypes. *American Journal of Botany* ,**76**:318~326.

Marshall,C. ,1990:Source-sink relations of interconnected ramets. In:Van Groenendael,J. ,de Kroon,H. (eds.). *Clonal growth in plants:regulation and function.* SPB Acad. Publ. ,The Hague,pp. 212.

Mooney,H. A. ,Field,C. ,1983:Photosynthetic characteristics of South African sclerophylls. *Oecologia*,**58**:398~401.

Pitelka,L. F. ,Ashumun,J. W. ,1985:Physiology and integration of ramets in clonal plants. In:Jackson,J. B. C. ,Buss,L. W. ,Cook,R. E. (eds.). *Population biology and evolution of clonal organisms.* Yale University Press,New Haven. pp. 565.

Schieving,F. ,Werger,M. J. A. ,Hirose,T. ,1992:Canopy structure,nitrogen distribution and whole canopy photosynthetic carbon gain in growing and flowering stands of tall herbs. *Vegetatio*,**102**:173~181.

Steel,R. G. D. ,Torrie,J. H. ,1960:Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill,New York.

Ueda,K. ,1960:Studies on the physiology of bamboo,with reference to practical application. Bulletin of the Kyoto University of Forestry,**30**:1~169.

Van der Toorn,J. ,Mook,J. H. ,1982:The influence of environmental factors and management on stands of *Phragmites australis* 1. Effects of burning,frost and insect damage on shoot density and shoot size. *Journal of Applied Ecology*, **19**:477~499.

Ye Zhiyun,1988:Studies on the relationship between the number of new shoots and density of stands in *Phyllostachys pubescens. Bamboo Research*(China),**7** (4) 61~64.