Front. For. China (2006) 2: 142–149
DOI 10.1007/s 11461-006-0014-8

RESEARCH ARTICLE

Zhang Yunchun, Du Xiaojun, Zhang Qiaoying,
Gao Xianming, Su Zhixian

Fitness analysis of seed and vegetative reproduction of clonal tree *Symplocos laurina*

Abstract There are two ways for *Symplocos laurina* to propagate: clonal reproduction and sexual reproduction. *S. laurina* adopted different ways to propagate and occupy space in different environments: under conditions with abundant water, nutrient resources, and lower light such as in an evergreen broad-leaved or a bamboo forest; survival rates and the ability of both clonal and sexual seedlings to occupy space, were relatively high. But clonal ramets took advantage both in terms of number and space. Therefore, clonal propagation predominated in such an environment. However, in habitats lacking sufficient nutrition and with higher light intensity, survival rates and space-occupying ability of two kinds of seedlings (sexual and asexual produced) were low and the space would be preempted by grown-up plantlets. A bottleneck in sexual propagation appeared at the stage from seed to seedling, while in clonal propagation it appeared during the period from an asexual plantlet to a ramet. The way *S. laurina* invaded space was like that of a plantlet settled in a place and then occupied the space rapidly by clonal growth under conditions of abundant water and nutrient resources and lower light such as in an evergreen broad-leaved forest or a bamboo forest. Clonal seedlings showed a great advantage in the initial stages, but this advantage disappeared after 15 years.

Keywords clonal plant, clone population, clonal propagation, distribution pattern, box dimension

Translated from Chinese *Journal of Applied Ecology*, 2005, 16(9)
[译自: 应用生态学报, 2005, 16(9)]

Zhang Yunchun (✉), Du Xiaojun, Gao Xianming
Laboratory of Quantitative Vegetation Ecology, Institute of Botany, Chinese Academy of Sciences,
Beijing 100093, China
E-mail: zhangyc@cib.ac.cn, xmgao@ibcas.ac.cn

Zhang Yunchun, Zhang Qiaoying
Chengdu Institute of Biology,
Chengdu 610041, China

Zhang Yunchun
Shandong Institute of Light Industry,
Jinan 250100, China

Su Zhixian
Mianyang Teachers' College,
Mianyang 621000, China

1 Introduction

In recent years, great progress has been made in clonal plant population ecology, which mainly focuses on integration of clonal plants (Pitelka, 1985; Alpert and Mooney, 1986; Schmid, 1987; Wang and Gai, 1995; Alpert, 1996; Dong, 1996; D'Hertefeldt and Jónsdóttir, 1999), plasticity of clonal plants (Wang and Gai, 1995; Alpert, 1996; Dong, 1996; Yang and Yang, 1997; Luo and Dong, 2002; Chen et al., 2003; Chen et al., 2004; van Kleunen and Fischer, 2005), growth models of clonal plants (Cain, 1990; Milletae, 1992; Chen et al., 1999), and survival predominance (Jiang and Dong, 2000). Most of the clonal plants are herbs, bamboo, or shrubs, and a few of them related to tree species. Research on clonal trees will enrich forestry studies and theories of clonal plants. *Symplocos Laurina* is a small evergreen tree, which is mainly distributed in the understory of forests at lower elevations. It has two propagation methods: clonal reproduction and sexual reproduction. Currently, there are a few studies conducted in this area, although some autecological research is under way. In this paper, age structure, growth status, and distribution patterns of young *S. laurina* in different habitats have been compared, with the purpose of studying the fitness of clonal reproduction and sexual reproduction in different environments and to find the causes and to discuss the special effects of this special species on forest regeneration.

2 Study site and methods

2.1 Study site

The experiment was conducted in the Banruo Temple forests of Dujiangyan city (31°41′–31°42′N, 103°3′–103°4′E) at an elevation of 740 m. It is warm and wet, the mean annual temperature is about 10°C; the average temperature is 6°C in January and 28.5°C in July and the annual cumulative temperature is 4,677.1°C. The main vegetations in the area are evergreen broad-leaved forests (Chen, 2000).

Given the existing vegetation types, three plots were selected, each 30 m×30 m, not far from each other. 1) In the *Neosinocalamus affinis* forest, the dominant plant is *N. affinis*, with some *S. laurina* and *Cyclobalanopsis glauca*. The soil is fertile and has been cultivated for a long time before planting *N. affinis* in 1949. 2) In the evergreen broad-leaved forest, the dominant trees are *Castanopsis fargesii*, *Lithocarpus harlandii*, *C. glauca,* and *S. laurina* with some *Quercus variabilis*, *Cornus controversa*, *Acer catalpifolium*, *Phoebe zhenman*, and others. The shrubs include *Piuosporum daphniphylloides*, *S. stellaris*, *Ilex purpurea,* and *Myrsinea fricana,* and the herbs *Isachne globosa*, *Lophantherum gracile* and *Dicranopteris pedata*. 3) In the coniferous and broad-leaved mixed forest, the dominant trees are *Q. variabilis*, *C. fargesii*, *C. glauca* and *L. harlandii*, while *Camellia oleifera* and *D. pedata* in the shrub and herb layers.

S. laurina is a small evergreen tree, only 4–12 m high, buds brown pubescent, petiole, 1–1.5 cm; leaf blade ovate-elliptic to obovate-elliptic, 6–21 cm×2–8 cm, leathery, glabrous; bracts and bracteoles persistent, margin glandular punctate, pubescent, ovaries not hidden; calyx glabrous, not enlarged in fruit; lobes semiorbicular 1–2 mm, shorter than tube; stamens ca. 30; drupe globose, 4–6 mm in diameter, apex with persistent erect calyx lobes. It flowers from August to December and yields fruits from March to June. The tree is mainly distributed in east, southeast, and southwest China and can also be found in Vietnam, India, and Sri Lanka (Institute of Botany, 1974; Editor Committee for *Flora of Sichuan*, 1981). *S. laurina* is the principal tree species or even the climax species in subtropical evergreen broad-leaved forests (Guo et al., 1997). The species is important both in the tree and shrub layers (Ma et al., 2002) and, therefore, very important for the regeneration of evergreen broad-leaved forests.

2.2 Methods

2.2.1 Sampling

Three typical populations of *S. laurina* were selected in an evergreen broad-leaved forest, in a coniferous and broad-leaved mixed forest and in a bamboo forest during August, 2001. Environmental factors, including transmittance (ZDS-10 digital illuminometer), gradient, aspect, soil humidity (0–20 cm) and soil organic matter (0–20 cm), were measured in all plots. Each plot was divided into 36 adjacent 5 m×5 m sub-quadrants and the number of clonal seedlings and young grown-up plantlets of *S. laurina* in each sub-quadrant was counted. Age, base diameter, or diameter at breast height and crown diameter of each clonal seedling and grown-up plantlets were recorded carefully. A site occupancy map of each clonal seedling and grown-up plantlet was drawn.

2.2.2 Data analysis

Data were analyzed by Excel. The following activities were carried out: 1) The total number of plants, clonal ramets and grown-up plantlets and ratio of clonal ramets to grown-up plantlets were obtained or calculated for each plot; 2) The number of clonal seedlings, grown-up plantlets, and their percentages were tabulated by age group. 3) The number of clonal seedlings, grown-up plantlets, and their percentages were obtained or calculated by height and crown diameter. For easy comparison, crown diameter was the mean diameter taken from two different directions; 4) Height and crown diameter of clonal seedlings and grown-up plantlets of the same age, in different habitats, were counted.

The box fractal dimensions were calculated as follows:

$$D_b = \lim_{\varepsilon \to 0} \frac{\log(N(\varepsilon))}{-\log(\varepsilon)} \quad (1)$$

where D_b is the box dimension; plots were divided into a series of grids with different circumferences (ε) and their respective coverage values were calculated; the number of non-blank grids (N) was counted (Ma and Zu, 2000; Ni et al., 2000).

3 Results

3.1 Quantitative characteristics of *S. laurina* populations in different habitats

The characteristic measurements made are presented in Table 1. From Table 1 it is seen that most *S. laurina* trees were found in the evergreen broad-leaved forest with higher canopy cover; fewer trees were found in the bamboo forest with a higher ground water table and better fertility; the smallest number of trees were found in the coniferous and broad-leaved mixed forest with little soil water, low fertility, and strong sunlight. The frequency of occurrence of clonal ramets (%) by forest type is as follows: bamboo forest (86%) > evergreen broad-leaved forest (72%) > coniferous and broad-leaved forest (39%). There are more grown-up plantlets in the evergreen broad-leaved forest than in the bamboo and coniferous and broad-leaved mixed forests; the percentages were: coniferous and broad-leaved mixed forest (61%) > evergreen broad-leaved forest (28%) > bamboo forest (14%). The ratio of clonal ramets to grown-up seedlings in the coniferous and broad-leaved mixed forest was smaller than 1 (0.634), and thus, sexual reproduction was the main method of reproduction. Both the ratio of clonal ramets to grown-up seedlings in bamboo forest and evergreen broad-leaved forest are larger than 1, 6.351 and 2.603, respectively and clonal reproduction was the main method of reproduction.

Table 1 Quantitative characteristics of *S. laurina* populations in different habitats

Sample	Total plants	Clonal ramets	%	Grown-up plantlets	%	CR/GS	Slope gradient	Slope aspect	Soil water content	Soil organic matter	Transmittance
A	69	27	39	42	61	0.634	26°	E	19±1.2	2.3±0.23	20.0±1.96
B	419	362	86	57	14	6.351	24.5°	SE35°	25.12±3.1	4.2±1.11	11.0±1.08
C	1,679	1,213	72	466	28	2.603	15.5°	SW9°	25.45±1.7	3.5±0.47	5.3±0.83

* CR: Clonal ramets; GS: Grown-up seedlings (the same as in the following tables). A: coniferous and broad-leaved mixed forest; B: bamboo forest; C: evergreen broad-leaved forest. The value of soil water content and soil organic matter and transmittance is mean ± s.e.

3.2 Age characteristics of populations in different habitats

Age level was formed with the ratio of the number of different age-class to the number of ramets (Table 2). From Table 2, the ratios of the two kinds of plantlets or seedlings are great in three forest types. The number of clonal plantlets is large except for coniferous and broad-leaved mixed forest, and the percentage of sexual seedlings, although still large, is much less than that of clonal plantlets. The number of age-class of the two kinds of plantlets in the three forest types both follows the order of evergreen broad-leaved forest > bamboo forest > coniferous and broad-leaved mixed forest.

3.3 Growth characteristics of populations in different habitats

3.3.1 Characteristics of height and crown diameter

From Table 2, it is seen that all clonal ramets in the coniferous and broad-leaved mixed forest occurred at a height below 1.5 m, of which 88.9% were found below 1 m; grown-up plantlets occurred up to 3.5 in height and 66.7% were found below 1 m. In the bamboo forest, the ramets were found at heights lower than 2.5 m and the grown-up plantlets were found lower than 3.5 m, of which 87.0% and 63.1% were shorter than 1 m. Big plants, taller than 5 m were only found in the evergreen broad-leaved forest. The percentages of clonal ramets and grown-up plantlets shorter than 1 m were 87.3% and 66.5%.

Crown diameters of clonal ramets and grown-up plantlets in the coniferous and broad-leaved mixed forest were found at heights of less than 0.8 and 1.5 m, respectively, of which 96.3% and 83.4% occurred below 0.6 m. Those in the bamboo forest were found below 2.5 m, the crown diameter of grown-up plantlets were all found at heights greater than that of ramets (some well above 2.5 m), of which 97.8% and 72.0% were found below 0.6 m. Both the crown diameter of ramets and grown-up seedlings were bigger than those of ramets (many were taller than 2.5 m), of which 98.6% and 77.0% were smaller than 0.6 m respectively. Most of the seedlings were short and had small crown diameters in all three forests types. The levels of age and crown diameter of ramets are lower than those of grown-up plantlets.

3.3.2 Characteristics of height and crown diameter of populations with same age

In Table 3, we present the characteristics of *S. laurina* trees of the same age under different environmental conditions. From Table 3 it can be seen that young ramets are consistently taller than grown-up plantlets of the same age in different plots, and grow faster. Young grown-up plantlets were shorter and grew slower up to age 4–6 after which growth accelerated. At the end of the growth season, the growth rate and height of the two kinds of plantlets gradually became the same. Crown diameter and height characteristics of populations with the same age were similar in different habitats, but the growth of crown diameters of grown-up plantlets was delayed until they were about 9–11 years old.

3.4 Fractal character of spatial pattern in different habitats

Straight-line fitting is applied to grid circumstance (ε) and the number of non-blank grids (N) in double coordinates; the result shows a good fitness. The slope of fitting is box dimension of distribution pattern (Fig. 1, Table 4). The results show that the ability of clonal ramets and grown-up plantlets to occupy space are both greater in the evergreen broad-leaved forest than in the bamboo forest, which in turn is greater than that in the coniferous and broad-leaved mixed forest; box dimension of clonal ramets is bigger than that of grown-up plantlets in evergreen broad-leaved forest and bamboo forest, but box dimension of clonal ramets is smaller than that of grown-up plantlets in coniferous and broad-leaved mixed forest.

Table 2 Characteristics of age, height, and crown diameter of *S. laurina* populations in different habitats

Item		Coniferous and broad-leaved mixed forest				Bamboo forest				Evergreen broad-leaved forest			
		CR	%	GS	%	CR	%	GS	%	CR	%	GS	%
Age /year	1	2	7.4	0	0.0	66	18.2	1	1.8	255	21.0	95	20.4
	2	2	7.4	2	4.8	103	28.5	5	8.8	243	20.0	42	9.0
	3	5	18.5	2	4.8	76	21.0	9	15.8	215	17.7	43	9.2
	4	8	29.6	6	14.3	41	11.3	4	7.0	169	13.9	52	11.2
	5	2	7.4	2	4.8	29	8.0	5	8.8	130	10.7	45	9.7
	6	1	3.7	2	4.8	22	6.1	3	5.3	76	6.3	40	8.6
	7	2	7.4	4	9.5	15	4.1	1	1.8	58	4.8	21	4.5
	8	3	11.1	2	4.8	4	1.1	4	7.0	27	2.2	26	5.6
	9	0	0.0	2	4.8	2	0.6	5	8.8	25	2.1	19	4.1
	10	2	7.4	2	4.8	2	0.6	2	3.5	8	0.7	10	2.1
	11	0	0	5	11.9	1	0.3	3	5.3	1	0.1	12	2.6
	12	0	0	3	7.1	0	0	1	1.8	1	0.1	15	3.2
	13	0	0	1	2.4	0	0	0	0	0	0	3	0.6
	14	0	0	3	7.1	0	0	0	0	1	0.1	3	0.6
	15	0	0	1	2.4	0	0	3	5.3	2	0.2	5	1.1
	16	0	0	0	0.0	0	0	0	0	1	0.1	11	2.4
	17	0	0	2	4.8	0	0	2	3.5	1	0.1	3	0.6
	18	0	0	2	4.8	0	0	2	3.5	0	0	6	1.3
	19	0	0	1	2.4	0	0	0	0	0	0	1	0.2
	≥20	0	0	0	0.0	1	0.3	7	12.3	0	0	14	3.0
	Total	27	100	42	100	362	100	57	100	1,213	100	466	100
Height /m	0–0.5	14	51.9	17	40.5	207	57.2	26	45.6	697	57.5	248	53.2
	0.5–1	10	37.0	11	26.2	108	29.8	10	17.5	361	29.8	62	13.3
	1–1.5	3	11.1	9	21.4	37	10.2	6	10.5	109	9.0	30	6.4
	1.5–2	0	0	2	4.8	9	2.5	5	8.8	36	3.0	38	8.2
	2–2.5	0	0	1	2.4	1	0.3	2	3.5	3	0.2	12	2.6
	2.5–3	0	0	1	2.4	0	0	6	10.5	1	0.1	15	3.2
	3–3.5	0	0	1	2.4	0	0	2	3.5	2	0.2	6	1.3
	3.5–4	0	0	0	0	0	0	0	0	2	0.2	14	3.0
	4–4.5	0	0	0	0	0	0	0	0	1	0.1	11	2.4
	4.5–5	0	0	0	0	0	0	0	0	0	0	10	2.1
	≥5	0	0	0	0	0	0	0	0	1	0.1	20	4.3
	Total	27	100	42	100	362	100	57	100	1,213	100	466	100
Crown diameter /m	0–0.2	10	37.0	11	26.2	86	23.8	23	40.4	370	30.5	243	52.1
	0.2–0.4	15	55.6	18	42.9	240	66.3	16	28.1	757	62.4	91	19.5
	0.4–0.6	1	3.7	6	14.3	28	7.7	2	3.5	69	5.7	25	5.4
	0.6–0.8	1	3.7	3	7.1	1	0.3	4	7.0	6	0.5	3	0.6
	0.8–1	0	0	2	4.8	1	0.3	0	0	4	0.3	5	1.1
	1–1.5	0	0	2	4.8	1	0.3	4	7.0	7	0.6	27	5.8
	1.5–2	0	0	0	0	2	0.6	3	5.3	0	0	21	4.5
	2–2.5	0	0	0	0	3	0.8	4	7.0	0	0	14	3.0
	≥2.5	0	0	0	0	0	0	1	1.8	0	0	37	7.9
	Total	27	100	42	100	362	100	57	100	1,213	100	466	100

Table 3 Characteristics of height and crown diameter of same age of *S. laurina* population in different habitats

Age /year	Coniferous and broad-leaved mixed forest				Bamboo forest				Evergreen broad-leaved forest			
	Height /m		Crown diameter /m		Height /m		Crown diameter /m		Height /m		Crown diameter /m	
	CR	GS	CR	GS	CR	GS	CR	GS	CR	GS	CR	GS
1	0.18		0.13		0.23		0.19		0.21	0.05	0.17	0.03
2	0.20	0.08	0.15	0.06	0.32	0.09	0.20	0.08	0.31	0.08	0.20	0.04
3	0.41	0.21	0.19	0.15	0.49	0.09	0.24	0.08	0.47	0.09	0.23	0.07
4	0.46	0.21	0.22	0.18	0.66	0.12	0.27	0.08	0.61	0.18	0.25	0.10
5	0.62	0.35	0.28	0.21	0.87	0.17	0.30	0.15	0.75	0.23	0.28	0.13
6	0.40	0.44	0.20	0.23	1.03	0.23	0.33	0.13	0.96	0.40	0.32	0.16
7	0.65	0.40	0.34	0.23	1.11	0.45	0.34	0.30	1.12	0.56	0.34	0.23
8	0.85	0.45	0.26	0.24	1.36	0.68	0.42	0.27	1.17	0.62	0.36	0.26
9		0.80	0.45	0.31	1.40	0.86	0.64	0.32	1.29	0.86	0.41	0.27
10	1.05	0.98		0.43	1.70	0.85	1.25	0.28	1.75	1.02	0.65	0.31
11		0.87		0.31	1.80	1.10	1.25	0.64	1.00	1.23	0.25	0.41
12		1.02		0.54		1.20		0.70	1.70	1.29	1.10	0.44
13		1.40		0.48						1.43	0.80	0.43
14		0.23		0.61					1.90	1.63	1.23	0.52
15		1.30		0.52		1.60		0.70	2.35	1.72		0.79
16				0.70					1.90	1.70	1.65	0.72
17		1.70				1.90		0.88	3.00	1.83	1.70	0.83
18		2.25		0.93		2.15		1.13		2.03		1.11
19										2.00		1.15
≥20		3.00		1.20	2.20	2.61	1.90	1.79		2.53		1.48

Table 4 Box dimension of distribution pattern of *S. laurina* population

Parameter	Evergreen broad-leaved forest		Bamboo forest		Coniferous and broad-leaved mixed forest	
	CR	GS	CR	GS	CR	GS
D_b	1.689	1.628	1.224	0.823	0.455	0.673
R	0.995	0.991	0.990	0.930	0.877	0.932

4 Discussions

4.1 Reproduction methods of clonal plants

There are two fundamental reproduction methods in the plant kingdom, i.e., sexual and clonal reproduction, both of which are available for many clonal plants (Richards, 1986; Zhang et al., 2001). Naturally, different habitats are usually the major cause leading to intra species differentiation, through both sexual and clonal reproduction (Wang, 2001). The new, young organisms resulting from these two reproduction methods have to occupy new habitats, but differ in strategies to accommodate themselves to their new environment (Zhang et al., 2001). For sexual reproduction, the plants depend more on themselves for survival and easily adapt to this new environment (Zhong, 1995; He et al., 1999). Clonal ramets have the advantage that nutrients still can be transported between ramets and mother plants. There is strong competition among plants in an environment with little or no disturbance; ramets can easily survive than grown-up plantlets and clonal reproduction is predominant in environmental selection (Grime, 1979). Clonal plants can spread quickly and use resources effectively, and so they can enlarge populations in the exploitation of new habitats and form the dominant population (Callaghan, 1988; Dong, 1996). The ratio of the two methods will change with different environments (Shea and Marc, 1999).

4.2 Quantitative characteristics of different reproduction methods of *S. laurina*

On an individual level, both clonal reproduction and sexual reproduction of clonal plants are occupied with generating new individuals and occupying new habitats (Zhong, 1995; Chen, 2000). Quantitative characteristics of clonal ramets and grown-up plantlets of *S. lauria* vary in different habitats (Table 1). The number of seedlings is bigger and clonal ramets are more predominant in humid, fertile, and closed habitats. The survival rate of both plantlets is very low and grown-up plantlets are predominant in dry, infertile environments with much sunlight. This shows up the different levels of fitness of clonal reproduction and sexual reproduction of *S. laurina* in different habitats: clonal reproduction is the principal form of reproduction in humid and fertile environments, otherwise sexual reproduction predominates, consistent with the conclusion reached by He et al. (1999). In addition, sunlight may be one of the important factors affecting the ratio of the two kinds of plantlets. If there is lack of sunlight, germination of seeds will be limited, and the ratio of grown-up plantlet to clonal ramets will be smaller.

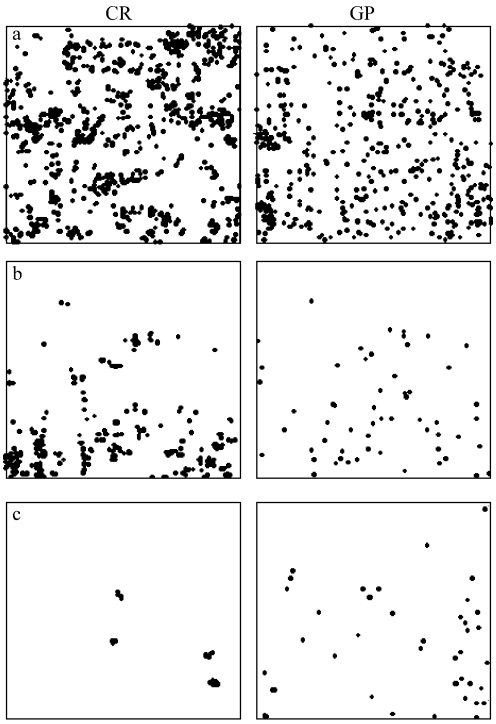

Fig. 1 Distribution pattern of *S. laurina* population (30 m×30 m). a) Evergreen broad-leaved forest; b) Bamboo forest; c) Coniferous and broad-leaved mixed forest; CR: clonal ramets; GS: grown-up seedlings.

4.3 Age and growth pattern of different reproduction methods of *S. laurina*

The number of young ramets is very big but sharply decreases with an increase in age; the number of grown-up plantlets also decreases with an increase in age but more slowly than that of ramets (Table 2). The reason for this is the integrated reproduction strategy of *S. laurina*'s clonal reproduction (Callaghan, 1988; de Kroon, 1991; Milletae, 1992; Wang and Gai, 1995; Alpert, 1996; Dong, 1996; Yang and Yang, 1997; Chen et al., 1999; Chen et al., 2003), i.e., the branches give birth to many ramets after they reach the soil. At the start of the growth period, each ramet needs only a little space, water, nutrients, and sunlight without competition for resources between ramets; thus they can grow normally. With the growth of ramets, each needs more resources and the competition for resources increases, which leads to mortality of some ramets. Grown-up plantlets through sexual reproduction are smaller in number and scattered, so that the competition for resources is smaller than that of ramets. The survival ratio of grown-up plantlets is higher. In other words, the bottleneck of the two reproduction methods is different; it is from seed to seedling for sexual reproduction and from seedling to mature plant for clonal reproduction.

Young ramets have height and crown width and the mother plants will foster for a while; so young ramets predominate in height, crown diameter, and rate of growth over grown-up plantlets (Table 3), which favor *S. laurina* to occupy space, water, and nutrients and defeat other species in competition for resources. At a later period of growth, the differences in the rate of growth between ramets and grown-up plantlets become small and in the end, height and the growth rate are nearly the same for both types of reproduction. The reason, for this is that, on the one hand, photosynthesis increases with the growth of grown-up plantlets and on the other hand, ramets have no access to mature plants and mature plants stop to foster ramets (Pitelka, 1985; Alpert, 1996; Dong, 1996; D'Hertefeldt and Jónsdóttir, 1999; He et al., 1999). Age-class of ramets is less than that of grown-up plantlets in all plots (Table 3), which shows that grown-up plantlets arise before ramets. That is to say, from occupying a new environment in which to settle down, grown-up plantlets invade first, then occupy space and use water and nutrients quickly in closed, wet, and fertile environments through clonal reproduction.

4.4 Fractal character of two reproduction methods of *S. laurina*

Box dimension reflects the spatial occupancy of fractals or the ability of a population to use eco-space (Ma and Zu, 2000; Ni et al., 2000). *S. laurina* uses various methods to occupy space in different habitats. From Table 4, it is seen that the box dimension of ramets is bigger than that of grown-up plantlets in the evergreen broad-leaved forest and the bamboo forest, while the reverse is true for the coniferous and broad-leaved mixed forest. It shows that both ramets and grown-up plantlets can grow better in a wet, fertile, and closed evergreen broad-leaved forest and bamboo forest than in a coniferous broad-leaved mixed forest. But *S. laurina* takes different reproduction methods to occupy space in different environments; clonal reproduction predominates in evergreen broad-leaved forest and bamboo forest with enough resources, while sexual reproduction predominates in coniferous broad-leaved mixed forest with less water and fertility and stronger sunlight. This is consistent with the quantity, age and growth characteristics of *S. laurina* populations, which showed that the box dimension could reflect the fitness of two reproduction methods of *S. laurina*.

5 Conclusions

Clonal reproduction and sexual reproduction formed during the evolution of *S. laurina* and the fitness of the two reproduction methods varied with different habitats. In this study, clonal reproduction predominated in habitats with enough water and fertility and high canopy cover, while sexual reproduction predominated in environments with less water and fertility and stronger sunlight. The bottleneck of the two reproduction methods is different; it is from seed to seedling for sexual reproduction, while from seedling to mature plant for clonal reproduction. *S. laurina* occupies a new environment by grown-up plantlets first by invasion and then occupies the space quickly through ramets because of the ease of clonal reproduction.

Acknowledgement This study was financially supported by the State Key Basic Research and Development Plan of China (Grant No. 2002CB111505 and G2000046802), the CAS Innovation Program (Grant No. KSCX-07-01-02), and the National Natural Science Foundation of China (Grant No. 39770134).

References

Alpert P. and Mooney H.-A., Resource sharing among ramets in the clonal herb *Fragaria chiloensis*. Oecologia, 1986, 70: 227–233

Alpert P., Nutrient sharing natural clonal fragments of *Fragaria chiloensis*, J. Ecol., 1996, 84: 395–406

Cain M.-L., Models of clonal growth in *Soloidago altissima*, J. Ecol., 1990, 78: 27–46

Callaghan T.-V., Physiological and demographic implications of modular construction in cold environments, In: Davy A.-J., Hutchings M.-J. and Watkonson A.-R. (eds), Plant Population Ecology, Oxford: Blackwell Scientific Publications, 1988: 113–135

Chen C.-D., The Dujingyan-Pivot sector of assemblage, differentiation and maintenance of biodiversity in northern part of Hengduan Mountain, Acta Ecol. Sin., 2000, 20(1): 28–34 [陈昌笃，都江堰地区——横断山北段生物多样性交汇、分化和存留的枢纽地段，生态学报，2000, 20(1): 28–34]

Chen J.-S., Dong M. and Yu D., The characteristics of stoloniferous herb *Fragaria vesca* L. ramet population and their variation along an altitudinal gradient in the eastern edge of the Qing-Zang Plateau in China, Acta Ecol. Sin., 2003, 23: 429–435 [陈劲松，董鸣，于丹，青藏高原东缘匍匐茎草本野草莓的分株种群特征及其沿海拔梯度的变化，生态学报，2003, 23: 429–435]

Chen J-S., Dong M., Yu D. and Liu Q., Clonal architecture and ramet population characteristics of *Lysimachia congestiflora* growing under different light conditions, Chin. J. Appl. Ecol., 2004, 15(8): 1,383–1,388 [陈劲松，董鸣，于丹，刘庆，不同光照条件下聚花过路黄的克隆构型和分株种群特征，应用生态学报，2004, 15(8): 1,383–1,388]

Chen S., Ma Y., Li Z-Z. and Wang G., Analysis and measurement of the fitness of seed reproduction and vegetative reproduction of clonal plant, Acta Ecol. Sin., 1999, 19(2): 287–290 [陈尚，马艳，李自珍，王刚，克隆植物种子繁殖和营养繁殖的适合度分析和度量，生态学报，1999, 19(2): 287–290]

D'Hertefeldt T. and Jónsdóttir I.S., Extensive physiological integration in intact clonal systems of *Carex arenaria*, J. Ecol., 1999, 87: 258–264

de Kroon, Resource allocation patterns as a function of clonal morphology: A general model applied to a foraging clonal plant, J. Ecol., 1991, 79: 519–530

Dong M., Clonal growth in plants in relation to resource heterogeneity: Foraging behavior, Acta Bot. Sin., 1996, 38(10): 828–835 [董鸣，资源异质性环境中的植物克隆生长：觅食行为，植物学报，1996, 38(10): 828–835]

Dong M., Plant clonal growth in heterogeneous habitats: Risk-spreading, Acta Phytoecol. Sin., 1996, 20(6): 543–548 [董鸣，异质性生境中的植物克隆生长：风险分摊，植物生态学报，1996, 20(6): 543–548]

Editor Committee for Flora of Sichuan, Flora of Sichuan, Chengdu: Sichuan People Press, 1981 [四川植物志编辑委员会，四川植物志，成都：四川人民出版社，1981]

Grime J.-P., Plant Strategies and Vegetation Processes, Chichester: John Wiley & Sons, 1979

Guo Q.-B., Liu Y.-C. and Li X.-G., The niche of dominant populations in forest secondary sere in Mt. Jinyun, J. Southwest Normal Univ. (Nat. Sci.), 1997, 22(1): 73–78 [郭全邦，刘玉成，李旭光，缙云山森林次生演替序列优势种群的生态位，西南师范大学学报(自然科学版)，1997, 22(1): 73–78]

He C.-Q., Zhao K.-Y. and Yu G.-Y., Advance in the ecology adaptability of the clonal plant in wetlands, Chin. J. Ecol., 1999,18(6): 38–46 [何池全，赵魁义，余国营，湿地克隆植物的繁殖对策与生态适应性，生态学杂志，1999, 18(6): 38–46]

Institute of Botany, Chinese Academy of Sciences, Iconographia Cormophytorum Sinicorum Tomus III, Beijing: Science Press, 1974 [中国科学院植物研究所，中国高等植物图鉴·第三册，北京：科学, 1974]

Jiang G.-M. and Dong M., A comparative study on photosynthesis and water use efficiency between clonal and non-clonal pant species along the Northeast China Transect (NECT), Acta Bot. Sin., 2000, 42(8): 855–863

Liu Q. and Zhong Z.-C., Clonal growth pattern of *Pleioblastus maculate* clone population, Chin. J. Appl. Ecol., 1996, 7(3): 240–244 [刘庆，钟章成，斑苦竹无性系种群克隆生长格局动态的研究，应用生态学报，1996, 7(3): 240–244]

Luo X.-G. and Dong M., Architectural plasticity of the stoloniferous herb, *Duchesnea indica* in response to different elevation, Chin. J. Appl. Ecol., 2002, 13(4): 399–402 [罗学刚，董鸣，匍匐茎草本蛇莓克隆构型对不同海拔的可塑性反应，应用生态学报，2002, 13(4): 399–402]

Ma D.-W., Zhang G., Wang Y.-H. and Wang D.-M., Studies on species diversity of forest vegetation on Qingcheng Mountain, J. Sichuan Univ. (Nat. Sci.), 2002, 39(1):115–123 [马丹炜，张果，王跃华，王道模，青城山森林植被物种多样性的研究，四川大学学报(自然科学版)，2002, 39(1):115–123]

Ma K.-M. and Zu Y.-G., Fractal properties of the spatial pattern of *Larix gmekini* population: box-counting dimension, Bull. Bot. Res., 2000, 20(1): 104–111 [马克明，祖元刚，兴安落叶松种群格局的分形特征：计盒维数，植物研究，2000, 20(1): 104–111]

Milletae L., Seasonal model of modular growth in plant, J. Ecol. 1992, 80: 123–130

Ni H.-W., Ma K.-M. and Zhao F.-C., The fractal character of the distribution pattern of *Deyeuxia angustifolia* population I. Box dimension, Bull. Bot. Res., 2000, 20(2): 229–234 [倪红伟，马克明，赵伏臣，小叶章种群分布格局的分形特征 I 计盒维数，

植物研究，2000, 20(2): 229–234]
Pitelka L.-F., Physiology and integration of ramets in clonal plants. In: Jackson J.-B.-C, Buss L.-W. and Cook R.-E., eds. Population Biology and Evolution of Clonal Organisms, New Haven: Yale University Press, 1985: 399–436
Richards A.-J., Plant Breeding Systems, London: George Allen & Unwin., 1986
Schmid B., Clonal integration and population structure in perennials: Effects of severing rhizome connections, Ecology, 1987, 68: 2,016–2,022
Shea N.-G. and Marc M., Modeling investments in seeds, clonal offspring, and translocation in a clonal plant, Ecology, 1999, 80: 1,202–1,220
van Kleunen M. and Fischer M., Constraints on the evolution of adaptive phenotypic plasticity in plants, New Phyto., 2005, 166 (1): 49–60
Wang R.-Z., Comparative study on clonal and sexual reproductive traits of *Leymus chinensis* populations in different habitats, Chin. J. Appl. Ecol., 2001, 12(3): 379–383 [王仁忠，不同生境条件下羊草种群无性系和有性生殖特征的比较研究，应用生态学报，2001, 12(3): 379–383]
Wang Y.-S. and Gai X.-C., Foraginhg growth patterns and resource allocation of clonal *Leymus Chinensis* population in the sungnen steppe, Acta Phytoecol. Sin., 1995, 19(4): 293–301 [王昱生，盖晓春，羊草无性系植物种群觅养生长格局与资源分配的研究，植物生态学报，1995, 19(4): 293–301]
Yang C. and Yang L., Influence of light intensity on differentiation and growth of *Leymus chinensis* clone, Chinese J. Appl. Ecol., 1997, 8(1): 83–87 [杨持，杨理，光强梯度对羊草无性系分化与生长的影响，应用生态学报，1997, 8(1): 83–87]
Zhang Y.-C., Su Z.-X. and Gao X.-M., Character and research of clonal plant, J. Sichuan Teach. Coll. (Nat. Sci.), 2001, 22(4): 338–343 [张运春，苏智先，高贤明，克隆植物的特性及研究进展，四川师范学院学报(自然科学版)，2001, 22(4): 338–343]
Zhong Z.-C., Reproductive strategy of plant populations, Chin. J. Ecol., 1995,14(1): 37–42 [钟章成，植物种群的繁殖对策，生态学杂志，1995, 14(1): 37–42]