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Spatial distribution patterns and environmental interpretation of *Anthriscus sylvestris* clonal buds

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Abstract *Anthriscus sylvestris*, a weed found both in Europe and China, is a kind of representative clustered clonal plant and is a foe on dams and banks. It has been widely investigated in Europe for its powerful progenitive ability and tolerance to severely adverse environments. Our aims were to investigate and quantify its spatial distribution patterns in four types of community habitats, using a clustering method and adjacency lattice established by Greig-Smith. We concluded our environmental interpretation based on canonical correspondence analysis (CCA) appended to a Monte Carlo test with randomized seeding. The results indicate that the buds around the parent roots are in an aggregation distribution pattern in all scales (0.002–5.12 m²), but theoretical distribution fitting, like negative binomial and Poisson distribution, show that some sizes of several sampling locations are out of place. For this, spatial ordination gives a satisfactory answer implying the effect of environmental variables such as depth of humus layer, soil moisture, light condition, disturbance intensity and herb abundance. CCA accounts for 64.7% of the total environmental variation and the remaining variation may be counteracted in those five variances or can be interpreted by other factors like accumulating temperature, annual rainfall and altitude in landscape scale. With the aid of temporal sequencing, the suppressed type II (monodominant) may be the former mode of suppressed type I (stable type), where invasion is done with the help of disturbance from both humans and nature. The abundance of *A. sylvestris* can add to our cognition in diversity resistance hypothesis and our hypothesis on disturbance before or upon immigration.

Keywords *Anthriscus sylvestris*, spatial distribution pattern, cluster clonal plant, canonical correspondence analysis, buds, ramets

1 Introduction

Module structure theory, its methods, and experimental studies on clonal plants have been widely investigated in the last few years (Yang et al., 2004). One of the consequences of these studies is the emphasis on spatial distribution patterns of plant populations, i.e., the biological characteristics of adaptation of a population to its habitat and, in the long run, to natural selection. It is one of the most important means of studying population and community characteristics, the interaction among populations, and the relationship between a population and its environment. Clonal plants spread vegetatively within their habitats by forming rooted ramets on stolons or rhizomes. Each of these ramets is capable of independent existence after establishment. Nevertheless, ramets remain connected physically by stolon or rhizome internodes for variable periods of time. It thereby allows for resource movement, signal transduction within clones, spatial patterns of plant communities and intensively competitive relations (Chao, 2002). However, information on the spatial pattern of bud modules is rare, especially on clustered clonal plants.

Anthriscus sylvestris (L.) Hoffm, a representative clustered clonal plant, is distributed in subtropical and temperate zones of China, mainly along the Yangtze River and the regions of Sinkiang and Inner Mongolia. It is not only a widespread species in Eurasia but also occurs in the temperate zone of North America (Roberts, 1979). Klinkhamer (1987) considered it a biennial, but it is essentially a kind of one-off flowering plant, for it will not be in a state of sexual reproduction in its second year if there is not enough nutrition. Only after access to ample resources will it bloom in the third or fourth year and generate buds which will turn into ramets. The parent material will die afterwards. *A. sylvestris* is common in Europe and is

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considered a bad weed (Parr and Way, 1988; Silvertown and Tremlett, 1989; Reader et al., 1992), for it randomly and diffusely distributes along river dams and lake banks if the environment permits, if there is sufficient nutrition, a damp soil and an intensively disturbed habitat. Further, it suppresses other herb species, especially shallow rooted grass, affects communities in a sensitive way, and decreases biodiversity and soil fertility, especially the humus layer as it diffuses using its powerful propagation ability (van Mierlo and van Groenendael, 1991; Reader et al., 1992; Sheng et al., 2002). It has similar characteristics as Baker weeds and has the potential ability to invade adjacent herbage communities using its ramets to hold the surface soil which is its main habitat. Invasive species, such as *A. sylvestris*, are serious threats to the environment and the economy. So what does this kind of potential advantage in invasion depend on? How will buds, modules and their dynamic spatial distribution be affected in the future when environmental factors intrude? It is, therefore, meaningful to study the buds sticking on roots when taking the bud as a module of the entire plant. We expect that *A. sylvestris* communities differ due to variations in abiotic and biotic conditions.

2 Methods

Community samples were taken from various places in the hills around West Lake, based on a full survey of *A. sylvestris* in Hangzhou, Zhejiang Province, China, with its representative subtropical climate. Altogether, there were eight samples, each with an area of 100 m². We intentionally took samples from different habitats, such as forest gaps, understory, hill sides or stream banks. We measured the buds in mid May when their numbers peaked, because first year plants cannot produce buds and those produced in the second year are old buds which clearly differ from their parents. Also, at this time it is easy to distinguish seedlings and buds (Sheng et al., 2004).

The depth of the humus layer, soil moisture content, light intensity, species abundance and intensity of disturbance were measured. The purpose of measuring the depth of the humus layer is that the root system of *A. sylvestris* develops mainly through the humus layer at a 1–5 cm depth, which determines its supply of nutrition. Fresh soil samples were taken back after several fine days and would last for more than 2–3 weeks. Each sample plot was divided into 16 sub-plots each with an area of 6.25 m². The soil samples were taken from the center of each sub-plot. The weight of fresh soil (S_f) was measured and the soil was kept under air-dry conditions until its weight remained constant (S_d). We calculated the average soil moisture (W_s). Soil samples were taken at irregular intervals at the two Lingyin plots because these were at the edge of a stream.

W_s was calculated by the following Eq. (1):

$$W_s = \frac{\sum_{i=1}^n (S_{fi} - S_{di}) \times 100\%}{n} \quad (1)$$

where n is the number of samples, $i = 1, 2, 3, \dots, n$.

We chose relative light intensity as the index of light conditions in the sample plots. Light intensity (L_m) was measured near noon (ca 10:00–14:00) under cloudy skies. The measuring points were the same as those of the soil samples. We took only ten samples at the Lingyin plots. Full sunlight intensity (L_a) was measured at a nearby open plot, at intervals of 5 min. The relative light intensity of the community (L_R) was then calculated by Eq. (2):

$$L_R = \frac{\sum_{i=1}^n (L_{mi}/L_{ai}) \times 100}{n} \quad (2)$$

In figures and graphs, we used the abbreviations LYD I and II for the Lingyin plots, SFCY for the ShuangFeng plot, STSD for the SanTai Hill plot, HILL I and II for the two Longjing Hill plots and TEMPLE I and II for the Longjing Temple plots.

The importance value (I_v) of the species was chosen to represent numerical characteristics, such as the abundance of companion species. Disturbance is the main cause of invasion (Holmgren et al., 2001). Parr and Way (1988) considered that two annual harvests are favorable for weed communities, but also offered the possibility that other herbs would be affected, as reflected by their importance values. Therefore, it was necessary to classify the degree of disturbance. In order to discover the effect of anthropogenic disturbance, we established three degrees of intensity, i.e., no human disturbance = 0, as in the LYD plots where small streams are randomly disturbed; human disturbance = 1, as in the SFCY plot, especially caused by the behavior of the occasional tourist; and disturbance of relative high intensity = 2, as in the TEMPLE, HILL and STSD plots, where disturbance is severe several times in early spring and late autumn.

Every index of spatial pattern analysis has its own advantages (Liu and Su, 2004), so it was important to select some appropriate aggregate indices which could provide useful information, estimated on spatial distribution patterns. These include the clumping index (C_i), the patchiness index (P_i) and the Morishita index (M_i). We used an adjacency lattice design, established by Greig-Smith (1983), and the mean variance test (MVT) to verify the scale of aggregation, and applied the Poisson distribution to study the theoretical discrete fit.

All data on environmental variables were subjected to a logarithmic transformation for standardization. Ward's method (group linkage method) and Euclidean distance were selected to investigate the ordination of communities, which were evaluated by five factors in our eight

samples. We used a random starting configuration with the number 322 as a seed for the random number generator. Canonical correspondence analysis (CCA) was employed to choose the best relationship of dimensionality: 1000 runs were performed with real data and 50 with randomized data that provided the basis for a Monte Carlo test of significance to compare the eigenvalues, which represented the relation with dimensions (axes). The stability criterion was set to 0.0010.

3 Results

3.1 Spatial distribution pattern in different habitats

3.1.1 Suppressed type I

HILL I, SFCY and TEMPLE II belonged to the suppressed type, where several tree species, such as *Cinnamomum camphora*, *Pistacia chinensis*, *Phoebe chekiangensis*, *Quercus acutissima* and *Quercus fabric*, covered the plots (Fig. 1). These trees have a high canopy density with a deep humus layer under the canopy. Normally, competition among species is intensive in the understory. *A. sylvestris* is distributed under a mixed forest canopy (composed of evergreen broad-leaved and largely defoliated trees), fragmented and limited to certain areas. Data showed that buds were in aggregation distribution between 0.002–5.12 m² scales in these three plots. Meanwhile, the fitted theoretical distribution implied that the species in HILL I and SFCY were randomly distributed under scales 0.002 and 0.005 m², which corresponded to a distribution around the roots of the parents. MVT showed that the aggregation scales of HILL I and SFCY reached their peaks under 0.005 m², and that of TEMPLE II was under 0.01 m² (Table 1). The second peak of those three plots did not appear, maybe due to an insufficient sample size (Greig-Smith, 1983). The aggregation scale of TEMPLE II was

larger than the other two plots because buds were disturbed more intensively where litter sweeping broke the aggregation at a small scale. As well, the importance value of *A. sylvestris* was high, corresponding to strong disturbance, while that of other herbs declined. Foraging behavior changed the propagation ability of the species to a kind of potential, given insufficient resources in these small heterogeneous habitats.

3.1.2 Suppressed type II

The difference with suppressed type I was that soil in the suppressed type II plots was so thin that there was almost no humus layer to provide enough nutrition to the clones. The considerably suppressed STSD and HILL II plots were at the edge of the forest or a road so that disturbance was intensive. The indices C_i and M_i showed that there was aggregation distribution under all scales. The fit of the theoretical distribution implied that the small scale distributions (0.002 m² of STSD and 0.002 m², 0.005 m² of HILL II) were random. The peaks of MVT are shown under the 0.002 m² scale (peak values = 0.094 and 0.112, respectively). *A. sylvestris* bloomed in the third or fourth year because of a lack of nutrients, and reproduction occurred sexually in both plots. Most of the emaciated buds could aggregate only around the roots of the parents pressed together and competed for limited resources. The nutrient distribution was even due to the function of the inner buds. Considerable disturbance favors *A. sylvestris* in competition, because its effect on the development of buds is small, so *A. sylvestris* could continue to absorb nutrients and develop leaves to support and compensate itself with photosynthesis (Bell, 1984) when disturbance occurs in the form of trampling under foot.

3.1.3 Invasive type

TEMPLE I belongs to the invasive type (Fig. 1). Representative species, such as planted *Iris proantha*

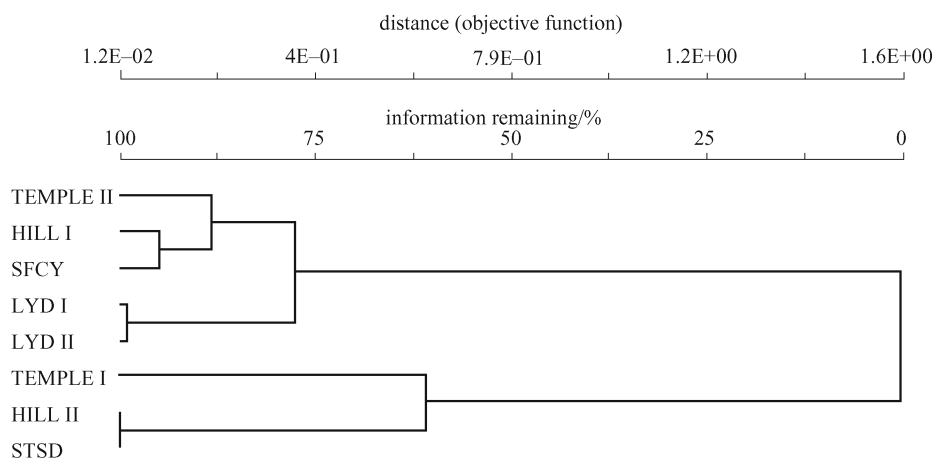


Fig. 1 Ward's relationship clustering method for communities of *A. sylvestris*

Table 1 Identification, distribution pattern and theoretical distribution of buds within *A. sylvestris* populations in different habitats

sample location	block size/m ²	variance	patchiness index	Morishita index		negative binomial		Poisson		pattern
				Morishita index	χ^2 test	χ^2 test	$\chi^2_{0.05}$	χ^2 test	$\chi^2_{0.05}$	
HILL I	0.002	0.073	112.304	114.099	37019.059	13.843	11.071	12.057	12.592	r
	0.005	0.104	197.225	192.323	21625.941	13.560	15.507	14.900	16.919	r c
	0.010	0.062	80.123	82.842	15514.102	4.661	21.026	28.259	22.362	c
	0.040	0.012	31.448	30.130	8929.900	6.904	18.307	30.881	19.675	c
	0.080	0.021	39.472	41.676	4663.423	8.003	24.996	27.114	26.296	c
	0.320	0.024	56.771	51.898	2698.340	10.428	30.144	36.307	31.410	c
	1.280	-0.023	3.697	3.667	1816.000	9.153	11.071	17.005	12.592	c
	2.560	0.013	4.025	4.001	3355.306	16.043	14.067	7.639	15.507	r c
	5.120		2.477	2.401	3201.421	13.337	11.071	16.475	12.592	
HILL II	0.002	0.112	203.912	201.443	41710.075	0.873	3.841	3.751	5.991	r c
	0.005	0.085	153.720	152.601	25311.429	7.461	9.488	9.342	11.143	r c
	0.010	0.067	100.387	99.567	17286.481	4.302	18.307	19.997	19.675	c
	0.040	0.047	50.471	51.421	8914.273	6.444	27.587	40.709	28.869	c
	0.080	0.026	43.687	43.002	5000.347	10.769	31.410	56.241	32.671	c
	0.320	-0.033	29.831	28.881	2771.847	18.475	26.296	31.472	27.587	r c
	1.280	0.026	5.776	6.007	1990.852	24.901	23.685	37.493	24.996	
	2.560	0.028	6.481	6.421	1733.201	11.798	21.026	30.141	22.362	c
	5.120		3.997	4.007	1274.153	3.881	11.071	27.448	12.592	c
TEMPLE I	0.002	0.041	89.241	90.411	35412.771	7.419	5.991	0.901	7.815	r
	0.005	0.094	142.638	134.578	21524.635	7.717	12.592	2.557	14.067	r c
	0.010	0.027	38.204	34.158	12707.919	3.471	24.996	21.476	26.296	r c
	0.040	0.013	27.962	27.009	8126.069	12.243	38.885	48.752	40.113	c
	0.080	0.012	11.158	10.482	4773.447	16.472	50.998	96.752	52.192	c
	0.320	0.008	10.703	9.887	3289.308	13.334	53.384	110.473	54.572	c
	1.280	0.013	3.423	3.394	2774.766	11.117	49.802	93.889	50.998	c
	2.560	0.005	2.685	2.640	1882.851	9.478	31.410	67.585	32.671	c
	5.120		2.319	2.253	1427.941	0.347	15.507	60.471	16.919	c
TEMPLE II	0.002	0.013	63.842	67.109	32481.155	0.033	3.841	26.677	5.991	r c
	0.005	0.034	96.475	93.334	20047.227	1.428	7.815	30.146	9.488	c
	0.010	0.087	112.301	111.715	14752.972	8.229	16.919	67.488	18.307	c
	0.040	0.071	42.101	45.265	9001.781	3.421	32.671	73.345	33.924	c
	0.080	0.033	24.249	25.336	4501.200	2.474	38.885	69.633	40.113	c
	0.320	0.014	15.263	16.472	2865.199	0.997	48.602	70.101	49.802	c
	1.280	0.029	7.412	7.862	1674.241	0.472	47.400	54.322	48.602	c
	2.560	0.046	9.118	10.001	1222.470	0.605	21.026	43.154	22.362	c
	5.120		6.331	6.205	993.071	1.074	12.592	33.906	14.067	c
SFCY	0.002	0.058	75.009	75.691	35436.422	9.249	7.815	2.062	9.488	r
	0.005	0.101	96.756	95.487	20437.510	2.599	15.507	5.608	16.919	r c
	0.010	0.022	41.154	42.015	13421.839	11.456	21.026	38.647	22.362	c
	0.040	0.023	24.664	24.607	7883.161	12.002	27.587	31.899	28.412	c
	0.080	0.015	17.058	15.478	7037.884	2.532	24.996	47.112	26.296	c
	0.320	0.019	6.451	6.515	4329.493	0.460	33.924	56.918	35.172	c
	1.280	0.006	5.600	5.547	3518.828	8.487	19.675	37.451	21.026	c
	2.560	0.017	4.217	4.129	2405.967	6.154	14.067	27.224	15.507	c
	5.120		4.551	4.516	2176.773	3.329	9.488	26.647	11.071	c
STSD	0.002	0.094	217.303	211.007	39472.041	1.071	3.841	5.076	5.991	r c
	0.005	0.082	150.417	153.222	26263.846	0.757	9.488	11.833	11.143	c
	0.010	0.066	94.258	97.459	17669.449	3.449	19.675	27.423	21.026	c
	0.040	0.018	76.240	77.143	8221.051	10.046	31.410	51.724	32.671	c
	0.080	-0.006	51.432	50.992	4736.044	8.497	37.652	58.438	38.885	c
	0.320	0.020	30.155	29.107	2010.338	5.012	40.113	60.251	41.337	c
	1.280	0.021	6.111	6.248	1930.460	3.307	30.144	67.456	31.410	c
	2.560	0.019	6.440	5.932	1562.376	12.478	21.026	49.321	22.362	c
	5.120		3.206	3.112	1029.442	12.967	11.071	35.260	12.592	
LYD I	0.002	0.373	96.347	97.024	23364.572	2.215	3.841	4.033	5.991	r c
	0.005	0.604	99.332	100.025	19224.257	4.008	7.815	6.124	9.488	r c
	0.010	0.551	81.174	82.729	13246.374	2.758	30.144	19.781	31.410	r c
	0.040	0.342	40.252	41.113	8914.454	8.366	32.671	36.337	33.924	c
	0.080	0.446	32.231	31.914	4426.170	11.429	19.675	39.076	21.026	c
	0.320	0.401	16.150	16.472	2841.363	15.693	21.026	30.208	22.362	c
	1.280	0.507	9.371	9.278	1515.261	16.300	12.592	18.115	14.067	c

(Continued)

sample location	block size/m ²	variance	patchiness index	Morishita index		negative binomial		Poisson		pattern
				Morishita index	χ^2 test	χ^2 test	$\chi^2_{0.05}$	χ^2 test	$\chi^2_{0.05}$	
LYD I	2.560	0.449	9.115	10.121	1141.231	15.227	9.488	12.766	11.071	
	5.120		6.055	6.205	1007.222	12.443	5.991	19.008	7.815	
LYD II	0.002	0.934	133.274	132.821	30015.721	3.005	3.841	27.632	5.991	r c
	0.005	0.732	110.622	108.423	19894.852	2.412	5.991	30.420	7.815	r c
	0.010	0.563	96.101	96.007	13789.519	3.088	18.307	38.441	19.675	c
	0.040	0.509	41.278	44.168	9346.946	7.337	30.144	67.142	31.410	c
	0.080	0.345	24.289	24.116	4362.997	6.052	38.885	90.471	40.113	c
	0.320	0.483	16.933	16.471	2966.302	11.638	19.675	88.553	21.026	c
	1.280	0.580	9.366	9.215	1830.422	5.534	16.919	42.996	18.307	c
	2.560	0.412	7.706	7.129	1162.342	2.798	11.071	41.213	12.592	c
	5.120		6.048	6.222	1019.335	1.728	11.071	16.086	12.592	

($I_v = 0.354$), was located in a part of a stream bank in the forest gap (about 50 m²) which also suffered from human disturbance. In this plot, *A. sylvestris* expanded quite fast because of good light conditions, a deep humus layer and high soil moisture. However, it was not the dominant species ($I_v = 0.9$) in the community, where the companion species were *Pilea cadierei* ($I_v = 0.998$), *Galium aparine* ($I_v = 0.317$), *Lamium* spp. ($I_v = 0.261$). Data showed that its aggregated distribution was between 0.002–5.12 m² scales and represented theoretically a random distribution between 0.002–0.01 m². To some degree, disturbance and the high quality of the habitat provided more living space for *A. sylvestris*, which implied that it could be distributed randomly under the scale 0.01 m². This type differed from TEMPLE II, both in length and diameter of the root of the parents. The buds at TEMPLE I were larger so that they expanded uniformly. MVT showed that there were two peaks (peak value = 0.094 and 0.013), although the second one at an aggregation of 1.28 m² was barely distinguishable from its segmented parents (the fragmented area was about 1–2 m²). Individual parents were spread by the stream and invaded this plot not long ago, and seedlings needed time to adapt to the habitat and settle down. High soil moisture, detrimental to seed germination (Sheng et al., 2004), is reflected in the difficulties encountered by seeds in space expansion. It is necessary to spend more time enlarging the population by asexual means in this plot.

3.1.4 Nature limiting type

Our special sample plots were usually inundated by water from the small streams, were rocky and barren, without any human disturbance and companion species, and were located where water from the small streams is the strongest natural disturbance. The aggregation indices C_i and M_i indicated this type of result at scales of 0.002–0.01 m² for the LYD I plot at an aggregation of 0.002–0.005 m² and with random distribution, as indicated by the theoretical fit

of the distribution, i.e., the possibility of resident seeds was small and the individual parents could not expand their living space by sexual reproduction. In an opposite manner, individual parents had accumulated more ramets and buds on a larger area (0.01 m²) over a long time. MVT showed two peaks presented under a scale of 0.002 m² and 1.28 m² in plot LYD I, while in plot LYD II, the peaks were presented at a scale of 0.005 m² and 1.28 m². In a natural ecosystem, the establishment of a seedbank of *A. sylvestris* is more difficult than for other species in the Umbelliferae family (Thompson and Baster, 1992). Because of erosion and obstruction by water from the small streams, shortage of suitable habitats and a low germination rate, *A. sylvestris* could aggregate in fragmented habitats that are the smallest in all of the sample plots. The choice of sample area and scale partition correctly expressed the second aggregation intensity under a scale of 1.28 m².

3.2 Environmental interpretation

Under the community scale, light density and depth of the humus layer were the definitive dominant factors of community clustering of *A. sylvestris*, while soil moisture was the main factor under the landscape scale. From the four types of habitats discussed, the ability to control propagation (distribution of buds and time of flowering) of *A. sylvestris* responded strongly to environmental differences, depending on the spatial distribution of nutrition under small scale.

CCA ordination explained cumulatively 64.7% of the environmental variation, where the first axis accounted for 29.6%, the second axis for 19.4% and the third for 15.7% (Table 2). A Monte Carlo test showed that the results from CCA are at least credible, according to the vector of eigenvalues ($p = 0.043 < 0.05$) and the vector of species-environment correlations ($p = 0.045 < 0.05$) (Table 3). The first axis was established based on light density ($r = 0.757, p < 0.01$) and the third axis was based on the depth of the humus layer ($r = -0.822, p < 0.01$) (Table 2).

The percentage of variation explained by the five environmental variables of the second axis was almost even, so that the ordination figure only need to show the first and third axes (Fig. 2). It was considered that a positive relationship ($r = 0.778$, $p < 0.01$) is implied between the depth of the humus layer and the importance index, I_v , in the four kinds of habitats because the development of weed will decrease with an increase in richness of other species in the community (Dukes, 2002). With the aid of a deep humus layer, the herbage community of the understory was stable, and the number of species was large, where *A. sylvestris* barely enlarged its living space without human or natural disturbance in the interaction among species and created an empty niche (Sher and Hyatt, 1999).

4 Discussion

According to a temporal point of view, the habitats of the suppressed type I and the invasive type, which were former modes of the suppressed type II, were suitable for *A. sylvestris* due to their abundance in nutrition and the presence of fewer companion species. From an evolutionary viewpoint, the foraging behavior of this clonal plant was neutral. *A. sylvestris*, a monodominant species, exerts its ability of intensive clonal strategy by means of intensive human disturbance, where native species retreat from community succession. The intensive clonal strategy was useful and powerful in expanding its living space (Bell, 1984). A high fruit-setting rate is the opposite of less biomass of floral organs, and a high seed germination rate (Roberts, 1979; Sheng et al., 2002, 2004) enables survival and propagation in adverse habitats, similar to habitats with sufficient nutrition after accumulation (suspending flowering for 1–2 years). Buds showed a stable strategy in improving endurance of the integrated system and absorbed available resources rapidly (Bell, 1984), as the buds in suppressed type II and the natural type did. Natural disturbances like water from small streams and rain helped spread seeds for a second time, adding to the rate of expansion. Under small scale communities, distribution is dependent on nutrition, light and humus. However, water was the main factor under the landscape scale. Clearly, environmental variables affect the numerical and spatial dynamic distribution of this species.

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