Acta Biologica Hungarica 66(3), pp. 282–292 (2015)
DOI: 10.1556/018.66.2015.3.4

COMBINED EFFECTS OF COLONIAL SIZE AND CONCENTRATION OF *MICROCYSTIS AERUGINOSA* ON THE LIFE HISTORY TRAITS OF *DAPHNIA SIMILOIDES*

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(Received: November 12, 2014; accepted: January 21, 2015)

Microcystis colonial size and concentration have detrimental effects on life history traits of *Daphnia*, but their detailed interactions have remained unclear so far. Our experiments show that the interaction between *Microcystis* colonial size and concentration on maturation time, life expectancy, net reproductive rate and innate capacity of increase in *Daphnia similoides* was significant. In all groups, the survival rate of *D. similoides* was 100% within 8 days. This value then declined quickly in the large-colony groups and in the SH group of *Microcystis*. Colonial *M. aeruginosa* significantly reduced the maturation time and body length at maturity of *D. similoides*. The number of offspring at first reproduction per female in the SH group of *Microcystis* was significantly higher than those in other groups. Net reproductive rate of *D. similoides* in the SL group of *Microcystis* was significantly higher than those in other groups of *Microcystis*. The innate capacity of increase of *D. similoides* in small-colony *Microcystis* groups was significantly higher than that in the large-colony groups. The results suggested that the effect of small-colony *Microcystis* on the reproduction of *Daphnia* was positive under lower concentration, while their toxicity was intensitied under higher concentration when small-colony *Microcystis* were by *Daphnia* as food.

Keyword: Daphnia similoides – Microcystis aeruginosa – innate capacity of increase – life history

INTRODUCTION

Microcystis is a bloom-forming cyanobacterium, which usually inhibits the growth and reproduction of large-body zooplankton (e.g., *Daphnia*) because of its colonial morphology, nutrimental shortage, and toxin production [2, 4, 6–7, 11, 18, 24].

The influence of colonial *Microcystis* on the growth and reproduction of *Daphnia* depends on both colonial *Microcystis* size and biomass. *Daphnia* could ingest single-celled and smaller-colony (60 μm to 100 μm) of *M. aeruginosa* [1–2, 5, 14], whereas larger-colony (100 μm to 150 μm) of *Microcystis* could not be utilized [14]. Higher colonial *Microcystis* biomass inhibited significantly population dynamics of *Daphnia carinata* in spite of *Microcystis* colonial size [8]. *D. carinata* dominated over small-bodied cladocerans in the lower *Microcystis* biomass (10 mg L^{-1} wet weight) but

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D. carinata disappeared in the higher *Microcystis* biomass (50 mg L^{-1}) [6]. However, little attention was paid to combined effects of colonial *Microcystis* size and biomass on the history parameters of *Daphnia*.

In some investigations, microcystin, as a hepatotoxin, is regarded as an important factor that *Microcystis* affects the growth and reproduction of *Daphnia*. Microcystin could delay maturation time and reduce the reproduction of *Daphnia* [4, 24]. The growth and reproduction of *Daphnia* declined as the proportion of the toxic *Microcystis aeruginosa* increased in the diet [7]. Moreover, the presence of toxic *Microcystis* increased the portion of available resources allocated to reproduction under diminished longevity in *Daphnia* [23].

The inhibitory influence of toxic *M. aeruginosa* on *Daphnia* might be restricted by other factors. Although the massive presence of toxic *M. aeruginosa* was lethal to *Daphnia pulex*, the toxicity of the cyanobacterium was significantly weakened by the presence of edible green algae *(Scenedesmus obliquus)* [19]. *Daphnia* populations that had prior experience with toxic *Microcystis* showed positive population growth in the presence of *Microcystis* [15, 24]. Gustafsson and Hansson [12] also observed that the capability of *Daphnia magna* to cope successfully with toxic *Microcystis* was improved if the animals were previously exposed to such cyanobacteria.

Although the effects of *Microcystis* on the growth and reproduction of cladocerans have been extensively investigated, limited attention has been directed toward the combined influence of colonial *Microcystis* size and concentration on the growth and reproduction of *Daphnia*. This study aims to determine the effects of *Microcystis* size, concentration, and their interactions on life history traits of *Daphnia similoides*, and discuss significant differences among different treatments of *Microcystis*.

MATERIALS AND METHODS

Lake Chaohu is a shallow, eutrophic, subtropical lake. It is one of the five largest freshwater lakes in China, with a total surface area of 780 km^2. Cyanobacterial bloom occurs in the lake every summer. Cyanobacteria are usually dominated by *Microcystis,* which produces microcystins [8, 16, 27].

D. similoides were collected from Lake Chaohu and cultured for approximately one year in an intelligent illumination incubator at 25 ± 1 °C. *Scenedesmus obliquus* were obtained from the Institute of Hydrobiology, Chinese Academy of Sciences, and were cultured in a Shuisheng IV medium [17]. The animals used in the experiment were neonates (<12 h old) incubated at 25 ± 1 °C, with an illumination of 2500 lx and a photoperiod of 12 h light: 12 h dark. Their food was 30 mg L^{-1} of *S. obliquus* (wet weight).

Colonial *Microcystis aeruginosa* was gathered from Lake Chaohu near Zhongmiao in July 2013. Previous studies indicated that *Microcystis* in Lake Chaohu produced microcystins MC-LR and MC-RR [8, 27]. Colonial *M. aeruginosa* was repeatedly washed with aerated tap water and filtered using a 112 μm net. The sample was divided into large- (≥112 μm) and small-colony (<112 μm) *Microcystis*. *M. aerugi-*

nosa was then transferred into a beaker to enable colonies to float on the surface layer. Separated *M. aeruginosa* were again rinsed thrice with aerated tap water. The collected *M. aeruginosa* was refrigerated at 4 °C during the experiment. No zooplanktons were observed in the microscope.

Two colonial *Microcystis* concentrations (5 and 20 mg L^{-1}, wet weight), two colonial sizes (≥112 and <112 μm), and one control group (not containing *Microcystis*) were selected. Five experimental treatments were used, namely, LH group (20 mg L^{-1} large-colony *Microcystis* + 30 mg L^{-1} *S. obliquus*), LL group (5 mg/L large-colony *Microcystis* + 30 mg L^{-1} *S. obliquus*), SH group (20 mg L^{-1} small-colony *Microcystis* + 30 mg L^{-1} *S. obliquus*), SL group (5 mg L^{-1} small-colony *Microcystis* + 30 mg L^{-1} *S. obliquus*), and CK group (30 mg L^{-1} *S. obliquus*). Each treatment had three replicates. The experiments were conducted in a 250 mL beaker that contains 200 mL of filtered (0.45 μm) tap water. Each beaker contained 10 neonates of *D. similoides* (<12 h old, with the 1.01 ± 0.09 mm of body length at birth). The experiments were conducted at 25 ± 1 °C under a 2500 lx light intensity and a 12 h light: 12 h dark photoperiod.

The culture solution was refreshed every other day before the animals became pregnant, after which the solution was refreshed daily. Maturation time and body length at maturity of *D. similoides* were observed and then measured with an Olympus microscope (×4 magnification). To obtain an accurate number of offspring at first reproduction, the pregnant animals were initially observed every 6 h under a microscope. Their numbers were counted after the birth of all offspring at first reproduction using a microscope. Then, the offspring produced were recorded daily. These offspring were promptly removed from the beakers.

The innate capacity of increase of *D. similoides* was calculated by using the following formula:

$$1=\sum_{x=0}^{n} e^{-rxl_x m_x},$$

where r is the innate capacity of increase (d^{-1}), l_x denotes the survival rate at x age, and m_x is the number of offspring at x age. Net reproductive rate (R_0) of *D. similoides* was calculated by

$$R_0 = \sum l_x m_x \text{ [26].}$$

SPSS20.0 statistic software was used to perform two-way ANOVA to analyze the influences of colonial *M. aeruginosa* size, concentration and their combinations on life expectancy, maturation time, body length at maturity, the number of offspring at first reproduction, and innate capacity of increase in *D. similoides*. Multiple comparisons were conducted using Tukey HSD to test the significant differences of each parameter among all treatments.

RESULTS

Effects of colonial M. aeruginosa *on the survival, growth and development of* D. similoides

The survival rate of *D. similoides* had obvious differences under different food combinations (Fig. 1). Among all groups, the survival rate of *D. similoides* was 100% before the eighth day of the experiment and then dropped. The survival rate of *D. similoides* dropped quickly in the LH group of *M. aeruginosa,* and the value was 40% at the twelfth day. However, a slow descent speed was observed in the SL group of *M. aeruginosa* and the control group (Fig. 1).

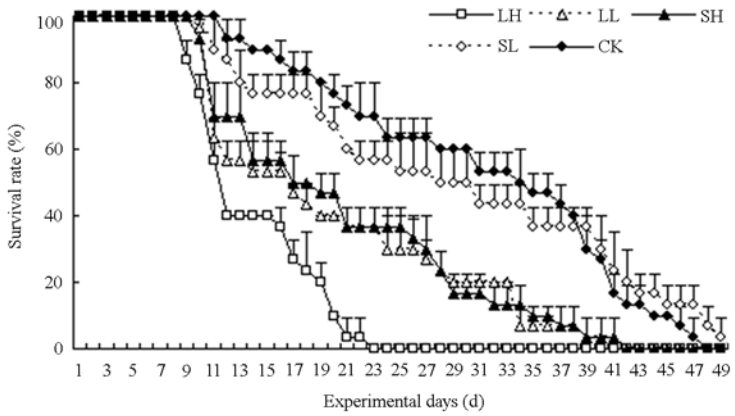

Fig. 1. Survival rate of *D. similoides* under different food combinations

Life expectancy of *D. similoides* in the SL group was significantly higher than that of the other groups containing *M. aeruginosa,* but no significant difference was observed when compared with the control group (Table 1, Fig. 2). The minimum (12.5 ± 0.5 d) appeared in the LH group. The interaction of *M. aeruginosa* colonial size and concentration significantly affected life expectancy of *D. similoides* (Table 1).

The maturation time of *D. similoides* in all treatments that contain *M. aeruginosa* was significantly lower than that of the control group. Among the small-colony *M. aeruginosa* treatments, the maturation time of *D. similoides* in the low-concentration group was significantly higher than that in the high-concentration group. However, no significant difference between the LH and LL groups was observed (Fig. 2). Two-way ANOVA showed that the interaction of *M. aeruginosa* colonial size and concentration significantly affected the maturation time of *D. similoides* (Table 1).

The presence of colonial *M. aeruginsoa* significantly reduced the body length at maturity of *D. similoides,* but no significant differences were found among all treat-

ments that contain *M. aeruginosa* (Fig. 2). Two-way ANOVA showed no significant effects with interaction of *M. aeruginosa* size and concentration on the body length of maturite *D. similoides* (Table 1).

Effect of colonial M. aeruginosa *on the reproduction of* D. similoides

In the LH group of *M. aeruginosa,* average offspring number of *D. similoides* produced by per female each day was at a low level (less than three individuals) during the experiment. In the LL and SH groups of *M. aeruginosa,* average offspring

Table 1
Two-way ANOVA shows the influence of colonial *Microcystis* size, concentration, and their combinations on the parameters of the growth and reproduction in *D. similoides*

Factors	*df*	SS	*F*	*P*
Life expectancy				
Microcystis size (A)	1	192.000	207.755	<0.001
Microcystis concentration (B)	1	159.870	172.988	<0.001
A×B	1	5.333	5.771	0.043
Error	8	7.393		
Maturation time				
Microcystis size (A)	1	1.517	55.232	<0.001
Microcystis concentration (B)	1	0.493	17.964	0.003
A×B	1	0.973	35.417	<0.001
Error	8	0.037		
Body length at maturity				
Microcystis size (A)	1	0.001	0.425	0.533
Microcystis concentration (B)	1	0.008	3.129	0.115
A×B	1	0.000	0.139	0.719
Error	8	0.021		
Per female offspring number at first reproduction				
Microcystis size (A)	1	5.603	30.986	0.001
Microcystis concentration (B)	1	4.563	25.235	0.001
A×B	1	0.163	0.903	0.370
Error	8	1.447		
Net reproductive rate				
Microcystis size (A)	1	4051.688	65.182	<0.001
Microcystis concentration (B)	1	5927.408	95.359	<0.001
A×B	1	941.641	15.149	0.005
Error	8	62.159		
The innate capacity of increase				
Microcystis size (A)	1	0.019	68.655	<0.001
Microcystis concentration (B)	1	0.001	4.598	0.064
A×B	1	0.002	5.363	0.049
Error	8	0.002		

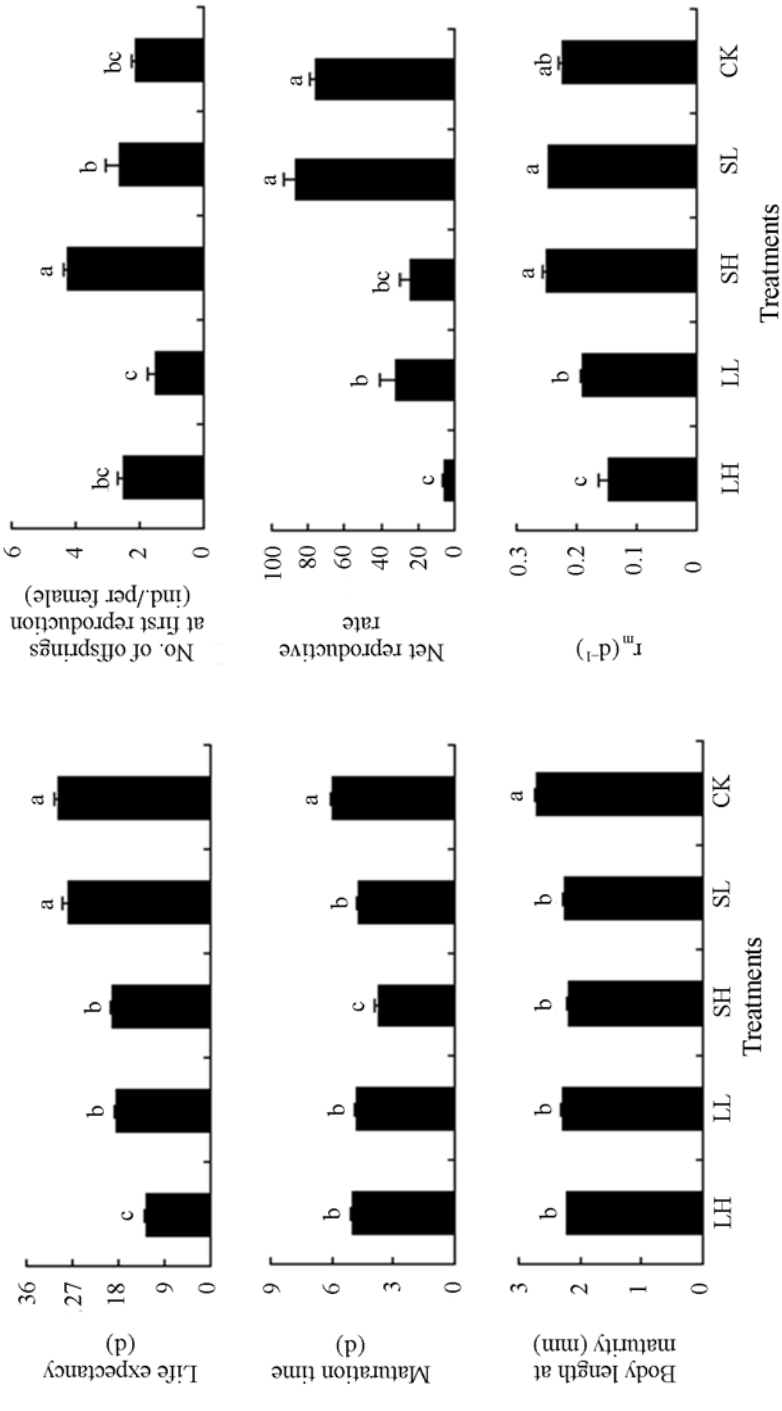

Fig. 2. Life expectancy, maturation time, body length at maturity, no. offspring at first reproduction, net reproductive rate and the innate capacity of increase (r_m) in *D. similoides* under different food combinations (mean±SD). *Note:* Different lowercase letters showed significant differences ($P<0.05$), same lowercase letters showed no significant differences ($P>0.05$)

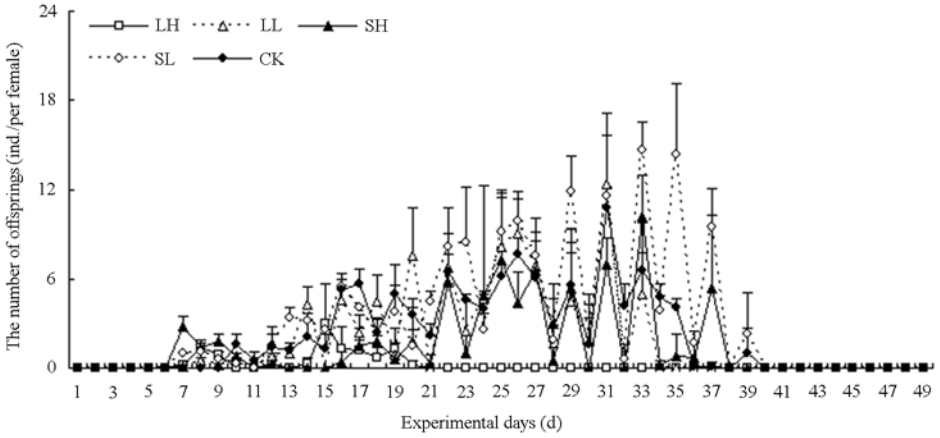

Fig. 3. Influence of different combinations of colonial *M. aeruginosa* and *S. obliquus* on the number of offsprings produced by per *D. similoides* female

numbers of *D. similoides* produced by per female each day were at higher levels after 14 d and 22 d until the experimental animals died out. However, in the SL group of *M. aeruginosa* and the control group, average offspring numbers of *D. similoides* produced by per female were at higher levels between 22 d and 37 d, but no or less offsprings were noted after 37 d (Fig. 3).

The number of offsprings at first reproduction per *D. similoides* female in the SH group of *M. aeruginosa* was obviously higher than that in other treatments. No significant differences were observed between the control group and three other groups that contained *M. aeruginosa* (Fig. 2). The influences of both size and concentration of *M. aeruginosa* on the number of offsprings at first reproduction of *D. similoides* were significant, but their interaction was not significant (Table 1).

Net reproductive rate (R_0) of *D. similoides* in the groups that contain *M. aeruginosa* were significantly smaller than that in the control group except in the SL group of *M. aeruginosa*. The maximum net reproductive rate (86.6±12.1) of *D. similoides* appeared in the SL group of *M. aeruginosa*. In spite of colonial size, high *M. aeruginosa* concentration significantly inhibited net reproductive rate of *D. similoides*. Two-way ANOVA showed that the interaction of *M. aeruginosa* colonial size and concentration affected significantly net reproductive rate of *D. similoides* (Table 1).

The innate capacity of increase in *D. similoides* in the small-colony treatments of *M. aeruginosa* was significantly greater than that in the large-colony treatments. No significant differences were observed between the small-colony treatments of *M. aeruginosa* and the control group. The innate capacity of increase in *D. similoides* in the LH group of *M. aeruginosa* was significantly smaller than that in the LL group (Fig. 2). Two-way ANOVA showed that the interaction of *M. aeruginosa* size and concentration affected significantly the innate capacity of increase in *D. similoides* (Table 1).

DISCUSSION

Colonial *M. aeruginosa* could not only interfere the ingestion of *Daphnia* but also affect their survival, depending on colonial size and biomass. The increase of colonial *M. aeruginosa* proportion in the mixed food treatment resulted in high juvenile mortality [13]. The survival rate of *D. carinata* was not affected by lower colonial *Microcystis* biomass (5 mg L^{-1}), but with the increase of *Microcystis* biomass (10–100 mg L^{-1}), survival of *D. carianta* were more intensely inhibited by small-colony *Microcystis* (<112 μm) than large-colony *Microcystis* (>112 μm) [8]. In this study, the survival rate of *D. similoides* was 100% within 8 d in all experimental groups and then declined obviously in the LH and LL groups of *M. aeruginosa*. It suggested that large-colony and high concentration of *Microcystis* strongly inhibited the survival of early-adult individuals of *D. similoides* through mechanical interference. However, the survival rate of *D. similoides* dropped quickly in the SH group in the late period of the experiment when the small-colony and toxic *M. aeruginosa* was utilized as food by *D. similoides*. Liu et al. [20] have also reported that toxic and colonial *Microcystis* could clog the pleopods of large cladocerans and cause their death after ingestion.

Many previous investigations had indicated that the body length of *Daphnia* declined with increased *M. aeruginosa* concentrations [7, 9, 18], including the body length at maturity [13, 21, 25]. Cerbin et al. [4] found also that increasing microcystin concentrations significantly reduced the body length at first reproduction of *D. pulicaria*.

During the study period, *M. aeruginosa* significantly restrained the body length at maturity of *D. similoides* despite colonial size and biomass, and no significant differences among all groups were observed. Colonial *M. aeruginosa* significantly shortened the maturation time of *D. similoides*, and the smallest appeared in the SH group. It suggested that colonial *M. aeruginosa* significantly inhibited the somatic growth of *D. similoides* regardless of colonial size and concentration while the small-colony and high concentration of *M. aeruginosa* significantly quickened the development of *D. similoides*. Han et al. [13] observed also that the maturation time of *D. galeata* reduced with increase of colonial *M. aeruginosa* percentage. However, Cerbin et al. [4] found that microcystin could significantly delay the maturation time of *Daphnia pulicaria*.

The function of *M. aeruginosa* on the reproduction of *Daphnia* was complicated and double. On the one hand, the response of *Daphnia* to *M. aeruginosa* was positive. Alva-Martínez et al. [1] found that *D. pulex* could ingest *M. aeruginosa* cells, which could then grow well in a manner similar to *Chlorella vulgaris*. In a Mexico reservoir, *Daphnia laevis* could utilize toxic and colonial *M. aeruginosa* and coexist with it [22]. Reinikainen et al. [23] observed that the presence of toxic *Microcystis* increased the portion of available resources allocated to reproduction under diminished longevity in *D. pulex*. Moreover, *Daphnia* populations that have prior exposure to toxic cyanobacteria may show positive population growth even at high concentrations of cyanobacterial toxins [24]. In this study, both the shortest maturation time and the

largest number of offspring at first reproduction of *D. similoides* appeared in the SH group of *M. aeruginosa*, which suggests that *D. similoides* could ingest small *Microcystis* colonies and allocate food resources to reproduction by shortening maturation time. As a result of both *D. similoides* and *M. aeruginosa* originated from Lake Chaohu, the reproductive adaptability of *D. similoides* to *M. aeruginosa* could be observed at the end of the experiment.

On the other hand, the inhibitory effects of *Microcystis* on the reproduction of *Daphnia* have been extensively reported in the laboratory [4, 7, 10, 24] and field [13, 18]. Ferrão-Filho et al. [10] have found that toxic *Microcystis* strongly reduced the population growth and reproductive output of five cladocerans (including three *Daphnia* species). Increasing microcystin concentrations could significantly reduce the number of offspring [4]. In subtropical reservoirs, the toxin and colonial morphology of *Microcystis* reduced net reproductive rate and intrinsic rate of population increase in *Daphnia geleata* [13]. The number of offsprings at first reproduction of *D. carinata* decreased with increasing *M. aeruginosa* biomass [25]. Some previous investigations had found that *M. aeruginosa* from Lake Chaohu contained microcystins, which it was toxic to *Daphnia* [3, 16, 27]. In this study, the number of offsprings at first reproduction in *D. similoides* in the SH group of *Microcystis* was significantly higher than that in all other groups, and the innate capacity of increase in *D. similoides* in the small-colony groups of *Microcystis* was significantly higher than those in the large-colony groups of *Microcystis*. Moreover, both the life expectancy and net reproductive rate of *D. similoides* in the SL group of *M. aeruginosa* were significantly higher than in other three groups that contain *Microcystis*. Therefore, it is likely that the effect of small-colony *M. aeruginosa* on the reproduction of *D. similoides* was positive under lower concentration, whereas the toxicity of microcystin was intensified under higher concentration when small-colony *Microcystis* were utilized by *D. similoides* as food. Deng et al. [8] have also found that the inhibitory effect of small-colony *M. aeruginosa* on population size of *D. carinata* was stronger than that of the large-colony one under higher biomass (50–100 mg L^{-1}) condition.

ACKNOWLEDGEMENTS

This work was supported by the National Natural Science Foundation of China (No. 31070387, 31370470), the Project of Anhui Key Laboratory of Resource and Plant Biology (No. ZYZWSW2014006) and the Natural Science Foundation from Educational Commission of Anhui Province (KJ2014B20).

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