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PLANT SEEDLING PERFORMANCE TRAITS IMPACT ON SUCCESSFUL RECRUITMENT IN VARIOUS MICROHABITATS FOR FIVE ALPINE *SAUSSUREA* SPECIES

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Abstract

Habitat heterogeneity and species-specific traits (seed mass) both impact on seedling performance and recruitment. Five species of *Saussurea* DC., from the Qinghai-Tibetan Plateau were selected to study seedling performance and recruitment under various microhabitats.. Results showed that seedling emergence and survival were significantly affected by light regimes, seed mass and their interactions. The RGR and R/S were affected by light and nutrient levels and seed mass during all growth stages. There was a significant interaction between nutrient and light on seedling survival. Light was directly related to seedling survival but nutrient availability was only indirectly related to seedling recruitment, by influencing the RGR and R/S ratio. Seedling survival was positively related to RGR and to R/S in the 100-day growth period. Our results suggested that seedlings improved their survival by altering their RGR and R/S under various microhabitats and the light and nutrient microhabitats affect seedling recruitment by impacting on seedling emergence and growth performance.

Introduction

Spatial heterogeneity widely affect the growth and survival of seedlings and may act as “filters” which affect species differentially (Harper, 1977). The fates of seeds and seedlings in different microhabitats determine seedling performance and establishment and therefore the period from seed to seedling establishment has important implications for grassland community dynamics (Welling & Laine, 2000, 2002; Rees *et al*., 2001; Cervera *et al*., 2006). Successful seedling recruitment may be affected by niche partitioning, niche differentiation or microhabitat specialization (Grubb, 1977). Anthropogenic disturbances, predation, litter burning, facilitation or competition from neighboring vegetation could all affect seedling survival and recruitment in alpine grassland communities (Caspersen & Kobe, 2001; Forbis *et al*., 2004; Cavieres *et al*., 2006; Chacón & Cavieres, 2008; Castro *et al*., 2010; Klanderud, 2010). These studies suggested that this may be related to disturbances that alter microhabitats (e.g., soil moisture, nutrient and light levels) where the seedlings are established. Light and nutrient availability are crucial factors that limit seedling growth and survival, particularly in the earlier growth stages.

Studies have shown that light and nutrient availability may limit the growth of plants once their seedlings have emerged (Rees *et al*., 2001; Moles & Westoby, 2004; Fenner & Thompson, 2005; Cervera *et al*., 2006). High and low levels of light both decreased seed germination, seedling growth and survival (Davis *et al*., 1999). In environmentally harsh habitats of low productivity, light and nutrient resources, competition during seedling growth may play an especially significant role in seedling survival and recruitment (Klanderud, 2010). These studies indicated that the potential for niche differentiation arises from differences among species in their responses to various combinations of environmental variables.

Meanwhile, studies have also found that seed bank densities were significantly larger than the field seedling densities in subarctic plant communities (Chambers, 1995; Welling & Laine, 2000; Forbis & Doak, 2004; Welling *et al*., 2004). Many alpine species also differed in abundance between seedling and adult stages because seedlings often had higher mortality rates during the winter than during the growing season (Forbis, 2003). Hence, it is important to study seedling emergence and growth to understand seedling survival and recruitment. Relative growth rate (RGR) and biomass allocation are major functional performance traits which are related to successful seedling establishment (Grubb *et al*., 1996; Coomes & Grubb, 2003; Weiner, 2004; Moles & Westoby, 2004). Species performance rankings for main fitness components (e.g., survival, biomass allocation or growth) were predicted to shift along microhabitat gradients (Fenner & Thompson, 2005; Klanderud, 2010). Plastic responses of plants (including changes in physiology, morphology, growth, life history and demography) can be expressed either within the lifespan of a single individual or across generations (Davis *et al*., 1999). Plants’ adaptive response to variable microhabitats by phenotypic plasticity such as those that regulate RGR, root to shoot (R/S) ratios or other morphological or physiological traits to achieve a trade-off between survival and growth (Hutchings & de Kroon, 1994; de Kroon & Hutchings, 1995; Matthes-Sears & Larson, 1999; Shipley & Meziane, 2002; Coomes & Grubb, 2003; Weiner, 2004; Xu *et al*., 2012). Recent experimental studies of seedling growth rates and survival under controlled conditions have investigated the effects of various combinations of light and nutrients, light and water (Cervera *et al*., 2006), or light, nutrients and water (Davis *et al*., 1999). Light scarcity because of competition among plants growing in high-densities was also considered a key factor for the failure of seedling recruitment in plant communities (Cervera *et al*., 2006; Yuan *et al*., 2012). Moreover, higher nutrient supplies also negatively affected seedling recruitment (Kitajima & Tilman, 1996; Foster & Gross, 1998; Stevens *et al*., 2004; Emery & Gross, 2007; Dickson & Foster, 2008; Eskelinen, 2010).

However, there are few studies that examine how species-specific seedling performance traits influence their survival in varying environmental conditions in the alpine area of the Qinghai-Tibetan Plateau while the effects of light and nutrient availability on seedling performance are better-known. Therefore, we conducted a pot experiment under field conditions where light and nutrient levels were controlled to investigate the relationships between seedling survival and performance for 5 *Saussurea* species. The main objectives of this study were: (1) to test the effects of light and nutrient availability on seedling recruitment and morphological performance traits for the five alpine *Saussurea* species; and (2) to study the relationship between seedling survival and seedling performance traits (relative growth rate and root to shoot ratio) during different growth stages under the various environmental conditions.

Materials and Methods

Study site: The study was conducted in Gannan state, Gansu province (35°58′ N, 101°53′ E, altitude ~ 3500 m), which lies at the northeast margin of the Qinghai-Tibet Plateau. The climate is humid-alpine with a mean annual rainfall of 620 mm, which is mainly distributed in summer. The mean annual temperature is 1.2°C ranging from -10.7°C in January to 11.7°C in July, the mean annual number of frost days is greater 270. The soil depth is about 80cm. The vegetation consists mainly of arctic alpine and Chinese Himalayan plants and is dominated by sedges (e.g. *Kobresia spp*.), graminoids (e.g., *Festuca spp*., *Poa spp*., *Agrostis spp*.) and composites (e.g. *Saussurea spp*.). The vegetation of the area is a typical alpine meadow (Wu *et al*., 2009, 2011a,b).

Study species: *Saussurea* DC. is one of the largest genera comprising over 300 species in the Asteraceae family (Bremer, 1994). The *Saussurea* species are a perennial herbaceous broad-leaf species that are typically the dominant species in the alpine meadow communities of the Qinghai-Tibetan Plateau. We selected five typical herbaceous plant species of the *Saussurea* genera from the Qinghai-Tibetan Plateau for this study (Table 1). All five species are widely distributed in the arid-environment of the mountainous area in the central and eastern part of Asia, especially in the Qinghai-Tibetan regions. They are adapted to a wide-range of habitats, such as meadow, scrubland, scree slopes & beaches, grassland, and riversides, in an altitude range of 200-6000m. Seeds were collected randomly in August to September, 2009, from more than 30 individuals for each species to get an adequate representation of the whole community in the alpine meadows of study region. Seeds of each species from different populations were collected and fixed. Ripe seeds were cleaned and stored at room temperature (~ 15°C) in paper envelopes (Kraft). All seeds were moist-cold stratified (about ± 4°C) for a month to break dormancy before the germination experiment. Seeds were allowed to air-dry to a constant mass at room temperature before being weighed. Seed mass was defined as the mass of the embryo and endosperm, plus the seed coat. Structures contributing to dispersal were not included as part of the seed mass (Table 1). Seeds were pooled per species, and five random subsamples of 100 seeds from each of the pooled samples were selected. Nomenclature and assignment to families followed Wu (1995).

Table 1. Summary of traits for the five studied species of *Saussurea* DC. and their relative abundance in alpine meadows.

Code	Species[a]	Air-dry seed mass/ seed[b] (mg)	Initial seedling dry mass / seedling[c] (mg)	Relative abundance[d]	Habitat
Smf	*Saussurea mongolica* (Franch.)	1.08 ± 0.007	0.7091 ± 0.0016	C	open meadow
Sb	*Saussurea bodinieri* Levl.	1.16 ± 0.009	0.7544 ± 0.0013	C	open meadow
Smc	*Saussurea morifolia* Chen	1.32 ± 0.005	0.7938 ± 0.0018	C	close meadow under woods
Sj	*Saussurea japonica* (Thunb.)	1.390 ± 0.004	0.9009 ± 0.0025	VC	open and close meadow
Si	*Saussurea iodostegia* Hance	3.31 ± 0.007	1.9693 ± 0.0045	VC	open and close meadow

[a] Nomenclature and assignment to families follows Wu (1995)

[b] Seed masses given as mean seed mass ±1 standard error per seed

[c] Mean initial seedling dry mass when the seedling's radicle length is equivalent to the cotyledon length

[d] Relative abundances of mature individuals of each species in alpine meadow habitats, based on survey: VC, very common species; C, common

Experimental design: The controlled outdoor pot experiment was conducted at a field research station of the northeast margin of the Qinghai-Tibetan Plateau from 25 April 2010 for 100 days, to study seedling emergence, survival and performance along ten gradients of resource availability (combinations of light and nutrient regimes), which reflect many different habitats for the plants that exist in the local grassland communities, e.g., ongoing desertification and dense growth of weed species following different disturbances lead to different levels of vegetation coverage, light regimes, and nutrients (Wu *et al*., 2009), which have created different microhabitats for seedling recruitment (Wu *et al*., 2011b). We placed pots in open ground where vegetation had been removed and fenced the experimental area to prevent grazing. The plot design for each treatment established the position of pots to receive 10 combinations of 5 light (L) and 2 nutrient (N) treatments (L100N10, L100N100, L150N10, L50N100, L25N10, L25N100, L10N10, L10N100, L4N10, L4N100). To control the amount of light, different densities of black plastic screening were used. For the 100% daylight treatment (L100), no screen was used, i.e., the screen density was zero. For the other four light treatments, the screens allowed the penetration of about 50%, 25%, 10% and 4% of full daylight (L50, L25, L10 and L4, respectively). The irradiance under each shade screen was measured using a Decagon Model SF80 Sunfleck Ceptometer (Decagon Devices, Inc. Pullman, Washington, USA) on a cloudless day. Thirty light measurements (photon flux density, $\mu mol\ m^{-2}\ s^{-1}$) using the single sensor setting were made for each irradiance regime. Full-strength Hoagland solution was used to establish the 2 nutrient treatments: N10 and N100 (by using a 10% and 100% solution of full-strength Hoagland solution, respectively) (Meziane & Shipley, 1999). Ripe seeds of each plant species were sown in plastic pots (40 cm × 40 cm × 50 cm) on the same day (25 April, 2010). The pots were all filled with fine-grained sand, which facilitated the later removal of the intact seedling root system from the pots. The sand was acid-washed three times before use to removal all nutrients, the pH of the water-saturated sand was about 7.1. To examine seedling emergence and survival proportion in the controlled microhabitats, 50 seeds of a given species were sown uniformly in a regular pattern to avoid competition and covered with a thin layer of sand in each pot, and 50 pots (5 replicates × 10 treatments) were used for each species. In another group of pots, in order to examine seedling growth performance, 10 seeds per species were sown in each pot and 100 pots (10 replicates × 10 treatments) were used for each species. From seed sowing, all pots were well watered during the entire germination and growth season and were given the same water volume every day in addition to normal rain. Hoagland's nutrient solution, according to the designated nutrient level, was added every 5 d after seedling emergence to ensure natural growth.

Seedling emergence was monitored each day and the exact location of the seedlings, which were tagged for ease of identification, on each pot surface was recorded. Seedling mortality was monitored daily after the first seedling emergence until the end of the experiment. The average seedling survival proportion at each growth stage (20, 40, 60, 80, and 100d after the emergence of seedling individuals) was noted, giving a standard measurement of seedling performance. Initial seedling dry mass was measured when the seedlings had barely emerged (Table 1). Further measurements were made at 20d after seedling emergences, and at 20d intervals thereafter for each species and treatment; these indicated that the five species were at similar developmental stages under the different microhabitats. Seven seedlings of similar size were harvested from 2 randomly selected pots for measurement per species per microhabitat. Seedlings were carefully washed with water to remove sand (especially the roots) and were oven dried (80°C) for 48h; dry biomass was determined by weighing on a precision electronic balance (0.0001 g accuracy). Biomass measurements included: seedling dry mass (g), above-ground mass (g), and root mass (g). The relative growth rate (RGR) and the root dry mass to above-ground dry mass ratio (R/S) was calculated from Causton and Venus (1981):

$RGR = (\ln Wt_2 - \ln Wt_1) / (T_2 - T_1)\ (g\ g^{-1} d^{-1})$

where Wt is the seedling dry biomass; T_2-T_1 is the time interval between measurements.

R/S = (root dry mass) / (above-ground dry mass)

Statistical analysis: Homogeneity of variance data on emergence, survival, RGR and R/S were checked for normality of distribution; no data transformations were required. The effects of light, nutrient and seed mass and their interaction effects were analyzed using ANCOVA of the General Linear Model (GLM) and Type III sums of squares, with light and nutrient availability as the fixed variables and seed mass as the covariate. Significant differences for all statistical tests were evaluated at the level of $p \leq 0.05$. Correlations among survival, RGR and R/S were calculated using parametric Pearson's correlation (*R*) with a threshold probability of 0.05, and considering the growth times in all the microhabitats. All analyses were made using SPSS 12.0 (SPSS Inc., Chicago, IL, USA) software.

Results

Seedling emergence and survival: The initial seedling size was significantly different among species, and the larger-seeded species had larger initial seedling biomass (F = 6.74, $p<0.01$; Table 1). Seedling emergence was significantly affected by the light regimes (F = 43.734, $p<0.0001$), species (F = 90.515, $p<0.0001$), and their interaction (F = 7.558, $p<0.0001$) (Table 2). Seedling emergence proportion decreased with the declining light regimes. Specifically, seedling emergence proportion of *S. mongolica* and *S. bodinieri* showed significant differences among different light regimes (Fig. 1). Emergence proportions of *S. iodostegia* and *S. morifolia* were greatest under 50% light availability (L50). The other three species had the greatest emergence proportion under 100% light conditions (L100) (Fig. 1). Seedling survival varied significantly among growth stages (Fig. 2). Species difference significantly affected seedling survival proportions during the latter stages except at 20d. During all growth stages, species difference and light all had significant effects on seedling survival proportions (Table 3). At 20d, 40d and 100d, light and nutrient levels had a significant interaction effect on seedling survival proportions.

Table 2. Results of three-way ANCOVA for the effects of seed mass (S), light (L), nutrient (N) and their interactions on seedling emergence proportion.

Source of variation	df[a]	F-ratio	p
S	4	90.515	<0.0001
L	4	43.734	<0.0001
N	1	1.172	0.282
S×L	16	7.558	<0.0001
S×N	4	1.892	0.118
L×N	4	1.365	0.252
S×L×N	16	0.855	0.621
Error	100		

[a] Degree of freedom (df); Significance level is $p \leq 0.05$.

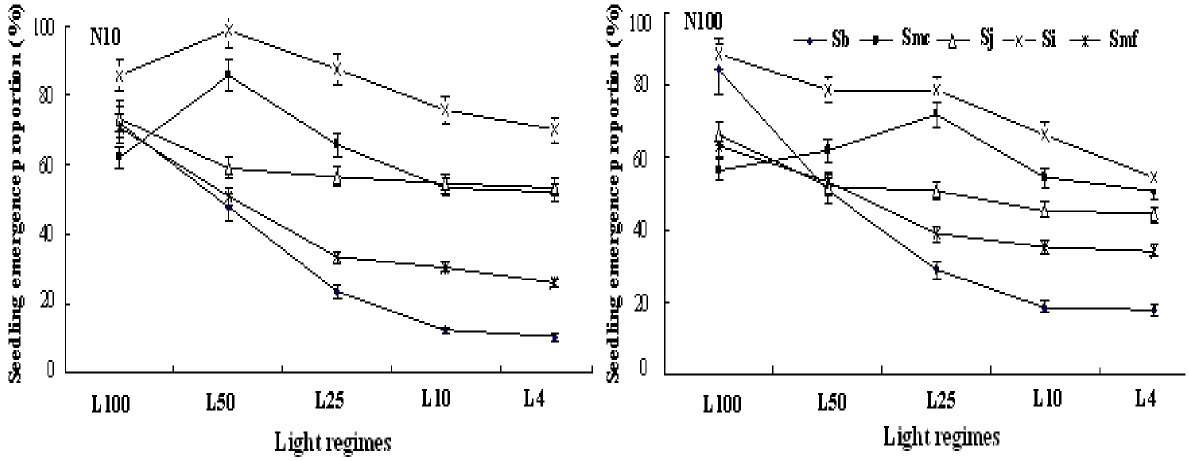

Fig. 1. Final seedling emergence proportion (%) of the studied *Saussurea* species in two nutrient (N100 and N10: plants received 100% and 10% full-strength Hoagland solution, respectively) and five light (L100, L50, L25, L10 and L4; numeral denotes percentage of sunlight received) regimes (Table 2). Data are presented as means (± standard error). Differences between all means were tested. Species: *S. mongolica* (Franch.), Smf; *S. bodinieri* Levl., Sb; *S. morifolia* Chen, Smc; *S. japonica* (Thunb.), Sj; *S. iodostegia* Hance, Si. The same below.

There were interaction effects between light and nutrient levels before 60 d and interaction effects between species and light after 60d on seedlings survival (Table 3). There were significant variations in seedling survival rates among the 5 species for all light regimes and growth stages. The maximum survival appeared mostly in the moderate light regimes (L50 or L25) during all growth stages. Initially, seedling survival was high under high and moderate light and was low under intense shade. During the later growth stages, seedling survival proportions appeared higher under moderate light regimes (L50 or L25) and higher nutrient availability (Fig. 2).

Relative growth rate (RGR): Seedling RGR was affected both by light, nutrient and species (Table 3). The RGR increased with light and nutrient availability (Fig. 3). The maximum RGR occurred under intermediate light levels (L50 and L25). After the first 20d, there were no significant differences among species. *S. morifolia* had the highest RGR in all the microhabitats, and *S. bodinieri* had the lowest RGR. The light and nutrient regimes both significantly affected the seedling RGRs. Seedlings of *S. bodinieri*, *S. japonica* and *S. mongolica* had maximum RGRs in the L50N10 and the L50N100 microhabitats. However, seedlings of *S. morifolia* and *S. iodostegia* had maximum RGRs in the L50N10 and the L25N100 microhabitats (Fig. 3). All species had low RGRs during the first 20d; the maximum RGR was at 40d, and then decreased with the increase of growth time. After 20d, species, and light and nutrient levels all had significant effects on RGR. Moreover, there was a significant interaction between species and nutrient level on RGR. Up to 60d, the light and nutrient levels also had significant interaction effects on RGR (Table 3).

R/S ratio: The R/S ratio was significantly affected by light and nutrient levels, and also by their interactions. There were significant interaction effects among species, and light and nutrient levels on the R/S ratio (Table 3). The R/S ratio increased with light availability and growth times, but decreased with nutrient availability. Also, there were significant differences among the R/S ratio of the species during all growth stages (Fig. 4). *S. morifolia* had the greatest R/S ratio in the L50N10 and the L100N100 microhabitats. *S. iodostegia* had its maximum R/S ratio at 80 d in the N10 microhabitats, but at 100 d in the N100 microhabitats. Similarly, *S. mongolica* had its maximum R/S ratio at 40 d in the N10 microhabitats, and at 100 d in the N100 microhabitats.

Relationship among seedling survival proportion, RGR and R/S ratio: Correlation analysis among seedling survival proportions, RGRs and R/S ratios showed that there was a significant positive relationship between seedling survival and RGR before 60 d, and, that the RGR was positively correlated with the R/S ratio. After 60 d, the RGR and the R/S ratio were both significantly and positively correlated with the seedling survival proportions (Table 4).

Discussion

Our results showed that seedling emergence and survival had significant differences in the light microhabitats and reached maximums under 50% light conditions (L50) for the studied species. These suggested that higher light regimes and the associated higher temperatures are both likely to constrain seedling recruitment in open microhabitats, which is a common seed regeneration niche in the tundra ecosystem (Shevtsova *et al.*, 2009). Disturbance is likely to affect multiple life stages and is most critical in seed germination and seedling establishment by indirectly affecting soil properties and microhabitats. Microhabitat variation can also affect seedling emergence and survival, and native herb diversity and abundance in the plant community (Castro *et al.*, 2010). Chacón & Cavieres (2008) reported that human disturbance significantly increased seedling recruitment in alpine vegetation of the Andes of Central Chile. Cavieres *et al.*, (2006) proposed that, in alpine plant community, cushion plants can facilitate seedling survival by providing them with the moisture that they have stored. Litter burning can also increase seedling recruitment of alien species and seedling richness in an alpine grassland community.

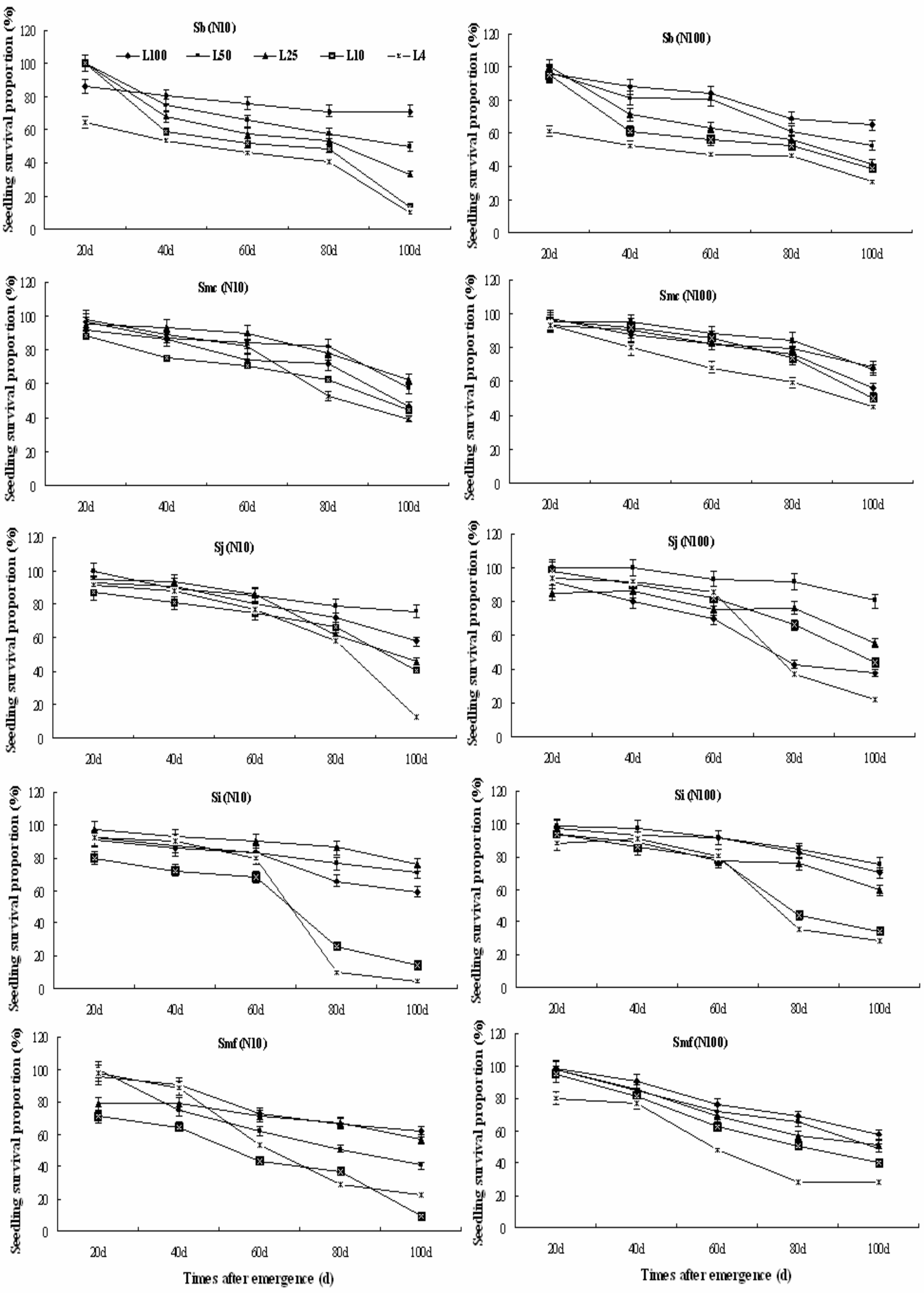

Fig. 2. Change in seedling survival proportion (%) over 100 days for the five studied *Saussurea* species. Data are the means (± standard error) of the corresponding proportion of surviving seedlings in different microhabitats having combinations of two nutrient and five light regimes.

Table 3. Summary of three-way ANOVA for the effects of seed mass (S), light (L), nutrient (N) and their interactions on seedling survival proportion, relative growth rate (RGR) and root to shoot ratio (R/S) of seedlings in five growth stages (20, 40, 60, 80 and 100 d).

		Survival			**R/S**			**RGR**		
Stages	**Parameters**	**df**	**F-ratio**	***P***	**df**	**F-ratio**	***P***[a]	**df**[b]	**F-ratio**	***P***
20d	S	4	1.389	0.243	4	36.140	<0.0001	4	2.858	0.058
	L	4	5.099	0.001	4	45.878	<0.0001	4	33.447	<0.0001
	N	1	1.009	0.318	1	57.055	<0.0001	1	8.049	0.012
	S×L	16	3.454	<0.0001	4	4.549	0.001	16	0.816	0.655
	S×N	4	0.697	0.596	16	3.213	<0.0001	4	1.585	0.227
	L×N	4	2.985	0.023	4	3.292	0.012	4	.379	0.820
	S×L×N	16	1.195	0.285	16	2.533	0.001			
	Error	100			300			16		
40d	S	4	11.418	<0.0001	4	34.106	<0.0001	4	12.332	<0.0001
	L	4	2.371	0.047	4	309.883	<0.0001	4	29.787	<0.0001
	N	1	4.851	0.030	1	207.281	<0.0001	1	32.708	<0.0001
	S×L	16	0.920	0.549	4	10.995	<0.0001	16	0.498	0.913
	S×N	4	0.313	0.868	16	10.891	<0.0001	4	6.440	0.003
	L×N	4	3.712	0.007	4	9.249	<0.0001	4	1.597	0.223
	S×L×N	16	0.594	0.882	16	4.166	<0.0001			
	Error	100			300			16		
60d	S	4	10.523	<0.0001	4	9.902	<0.0001	4	8.211	0.001
	L	4	2.911	0.025	4	163.271	<0.0001	4	14.955	<0.0001
	N	1	1.682	0.198	1	73.426	<0.0001	1	19.900	<0.0001
	S×L	16	0.968	0.497	4	3.560	0.007	16	2.160	0.067
	S×N	4	0.194	0.941	16	5.503	<0.0001	4	13.805	<0.0001
	L×N	4	2.163	0.079	4	2.954	0.010	4	0.759	0.567
	S×L×N	16	0.401	0.980	16	4.235	<0.0001			
	Error	100			300			16		
80d	S	4	6.579	<0.0001	4	34.974	<0.0001	4	4.435	0.013
	L	4	19.917	<0.0001	4	29.443	<0.0001	4	23.244	<0.0001
	N	1	2.020	0.158	1	72.407	<0.0001	1	1.061	0.318
	S×L	16	3.343	<0.0001	4	3.617	0.007	16	1.142	0.397
	S×N	4	0.682	0.606	16	2.371	0.002	4	2.910	0.021
	L×N	4	0.831	0.508	4	4.195	0.003	4	6.994	0.002
	S×L×N	16	1.056	0.407	16	3.120	<0.0001			
	Error	100			300			16		
100d	S	4	3.158	0.017	4	66.461	<0.0001	4	8.868	0.001
	L	4	37.211	<0.0001	4	53.184	<0.0001	4	22.274	<0.0001
	N	1	12.119	0.001	1	11.763	0.001	1	3.462	0.081
	S×L	16	5.153	<0.0001	4	3.566	0.007	16	2.031	0.084
	S×N	4	0.181	0.948	16	6.574	<0.0001	4	12.156	<0.0001
	L×N	4	3.110	0.019	4	16.524	<0.0001	4	3.737	0.025
	S×L×N	16	1.138	0.331	16	1.690	0.048			
	Error	100			300			16		

[a]Significance level is p≤ 0.05. [b]Degree of freedom (df)

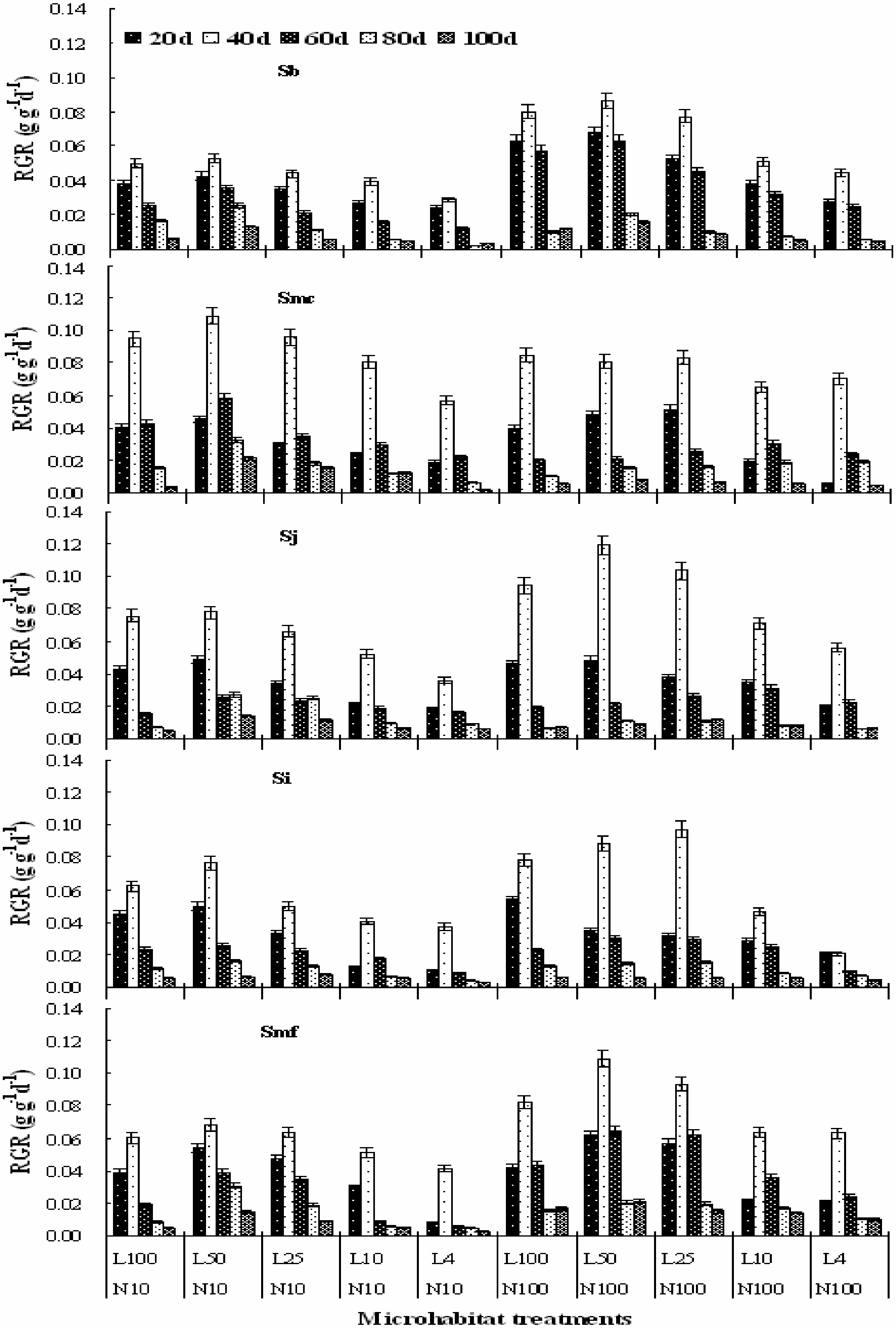

Fig. 3. Change in seedlings relative growth rate (RGR) over 100 days for the five studied *Saussurea* species. Data are the means (± standard error; n = 7) of seedlings in different microhabitats having combinations of two nutrient and five light regimes.

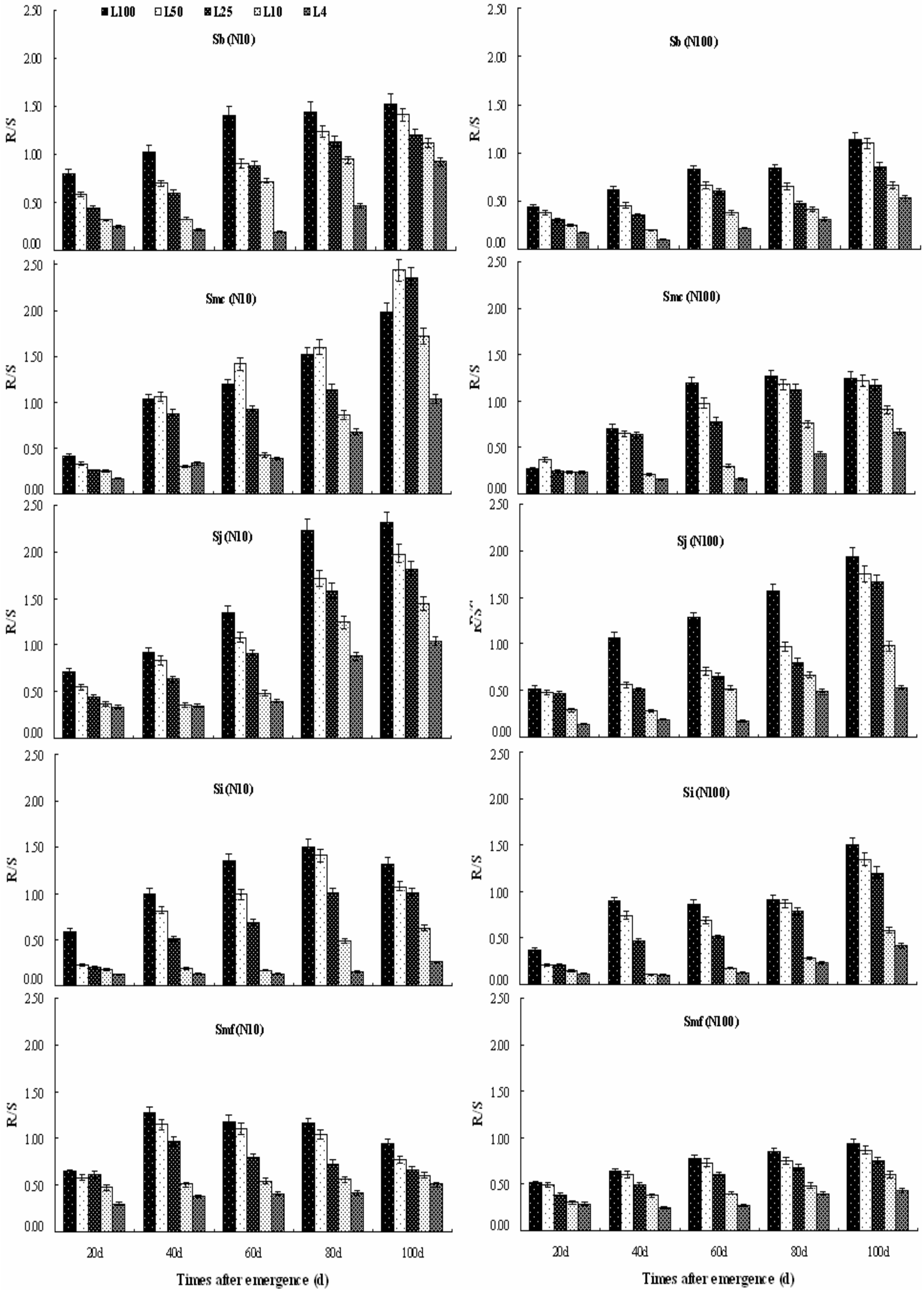

Fig. 4. Change in seedlings root to shoot ratio (R/S) over 100 days for the five studied *Saussurea* sp. Data are the means (± standard error; n = 7) of seedlings in different microhabitats having different combinations of two nutrient and five light regimes.

Table 4. Pearson's coefficients of correlations (*R*) for relationships among seedling survival proportion (Survival), root to shoot ratio (R/S) and relative growth rate (RGR) for different growth stage considering all the studied microhabitats.

		RGR		
20d	Survival	0.303*	Survival	
	R/S	0.501***	0.103ns	R/S
		RGR		
40d	Survival	0.440**	Survival	
	R/S	0.460**	0.289*	R/S
		RGR		
60d	Survival	0.149ns	Survival	
	R/S	0.225ns	0.304*	R/S
		RGR		
80d	Survival	0.467**	Survival	
	R/S	0.404**	0.584***	R/S
		RGR		
100d	Survival	0.338*	Survival	
	R/S	0.310*	0.535***	R/S

* $p<0.05$; ** $p<0.01$; *** $p<0.001$; ns $p>0.05$

Our study showed that seedling survival was significantly related to RGR and that RGR was also related to the R/S ratio at the initial seedling stages; the R/S ratio and the RGR jointly influenced seedling survival in mutative microhabitats. These results confirmed that successful seedling recruitment was significantly correlated with the RGR and with the R/S ratio. These growth performance factors would be related to the seedlings need to grow in order to reach light (Grubb *et al*., 1996). The growth performance responses of seedlings have significantly positive effects on seedling recruitment (Suding *et al*., 2003). Our study indicated that the RGR usually reached a maximum under moderate light conditions and not under the full sunlight regime (L100); and light is the key habitat factor that restricts seedling recruitment for these five studied *Saussurea* species. Thus, overly strong light radiation may decrease the seedling survival rate and recruitment by restricting the RGR in the alpine area of the Qinghai-Tibetan Plateau.

Response of biomass allocation and RGR is usually understood to be a consequence of changes in a plant's life-history strategy in response to the resource availability of its environment (Coomes & Grubb, 2003). Our study revealed important relationships between seedling recruitment and microhabitats. These results confirm that, for fitness traits (RGR and R/S ratio), the phenotypic response to the environment may be extraordinarily specific with respect to levels of interacting resources (Hutchings & de Kroon, 1994; Sultan, 2001). Also, seedlings had lower R/S ratios under shade conditions because plantsneeded to allocate biomass production to those parts that are responsible for acquiring the limiting resource, i.e. to shoots when light is limiting and to roots when nutrients or water is limiting (Bloom *et al*., 1985). It implies that seedlings develop fewer roots in shade than in sunlit conditions. Additionally, species-specific traits, such as seed mass, also affect the process of seedling regeneration under some microhabitats in plant communities (Welling *et al*., 2005). Small seeds are advantageous for dispersal, whereas intermediate seeds have a greater probability of germinating and of becoming established in closed vegetation. These factors suggest that species-specific performance to environmental sensitivity were related to their life history traits and seedling survival (Sultan, 2001; Welling *et al*., 2005; Cervera *et al*., 2006).

Our results suggested that seedling survival was positively related to species-specific performance traits (RGR and R/S ratio) during different growth stages under various environmental conditions. The physiological and morphological characteristics were considered to be crucial aspects of seedling survival in different microhabitats. Interspecific variation in seedlings survival, RGR and R/S ratio was manifested not only in the microhabitats (light and nutrient), but also because the species-specific traits had important effects. Since seedling performance was also highly correlated with these species-specific traits, such as specific leaf area, leaf longevity and photosynthetic capacity, they may also contribute to interspecific performance differences (Suding *et al*., 2003).

Additionally, our study found that seedlings adapt to the heterogeneous microhabitats by altering the R/S ratio, although the RGR of seedlings decreased with age. The different life-history strategies were used by plants during different growth stages. Also, the interaction effects of habitat factors (light or nutrient) and species-specific trait on seedlings growth alternate; the species-specific trait and nutrient availability have major influences at the initial growth stages while the species trait and light availability have major influences at the later growth stages. Our results suggested that light is directly related to seedling survival but nutrient availability is indirectly related to seedling recruitment, by influencing the RGR and the R/S ratio. This implied that light and nutrient availability both have significant effects on seedling recruitment in alpine meadows of the Qinghai-Tibetan Plateau. The different life-history strategies of species are composed of these complex adaptations by which the plants achieve improved fitness (survival or reproduction). However, further research is required to assess the effects of microhabitats on plasticity of seedling survival in order to understand the seedling recruitment mechanisms in alpine grassland communities. In mutative microhabitats, seedlings increased their RGRs to improve fitness at the early stages, but seedlings changed this strategy and improved their fitness (growth and survival) by increasing their R/S ratios at the later growth stages. A future study should examine the relationships of different life-history trait strategies of seedlings and success in their recruitment to more fully understand the basis of species differences in offspring recruitment and ecological distribution.

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