

## SEEDLING PERFORMANCE WITHIN EIGHT DIFFERENT SEED-SIZE ALPINE FORBS UNDER EXPERIMENTATION WITH IRRADIANCE AND NUTRIENT GRADIENTS

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### Abstract

Relative performance of seedlings of species with different seed sizes may vary in response to resource availability, and may affect seedling growth. The objective was to test this hypothesis from alpine forbs species in the Qinghai-Tibetan Plateau. We examined the relative growth rate, allocation and performances of eight native forbs species covering a wide range of seed size in response to four light and three nutrient regimes. Light availability had a significant effect on seedling emergence time, but not on other seedling morphological performances. Seedling emergence time and seed size were negatively correlated with each other for three species within *Asteraceae* family, i.e. heaviest seeds emerged earlier. Seed size, nutrient availability and their interaction affected most of studied morphological and growth traits of seedlings. Fertilisation modified the relationship between seed size and seedling biomass. Our study showed that seed size and nutrient availability had significant effects on seedling performance in alpine meadows. Seedlings from the larger-seed species presented stronger advantage in initial seedling mass and height under most of resources conditions.

### Introduction

The adaptive significance of phenotypic characteristics has interested ecologists for a long time (Bradshaw, 1965; Harper, 1977). However, many experimental studies have been recently performed to reassess and validate effect of seed size on seedling performance for plant species in recent years (Weiner, 2004; Miner *et al.*, 2005; Pigliucci, 2005). Performance may concern allocation of resources, the form of a plant part, rates of physiological processes and plant traits like seed dispersal, seed germination and seedling growth based on seed size. In this paper, we are particularly concerned with response of performance of seedling functional traits which include biomass, height, relative growth rate (RGR), specific leaf area (SLA), the leaf area ratio (LAR) and biomass allocation (Lavorel & Garnier, 2002; Cornellissen *et al.*, 2003; Violle *et al.*, 2007; Tang *et al.*, 2010). Much interest has centred on the question of whether or not species from resource-rich sites show greater response than species from resource-poor sites (Grime, 1979; Grubb, 1998), especially which seem against a background of variation in the availability of two or more resources. Recent experimental studies of germination have varied from one factor effect (light, nutrient and water supply) to two or more factors effects (Broncano *et al.*, 1998; Pearson *et al.*, 2002; Pearson *et al.*, 2003; Mumtaz *et al.*, 2010). And, recent experimental studies of growth rate and survival under controlled conditions tested the effect of light, nutrient and water availability variations (Grubb *et al.*, 1996, 1997; Walters & Reich, 1996; Meziane & Shipley, 1999; Sack, 2004) on naturally developing seedlings (Fukuhara & Shinwari, 1994; Caspersen & Kobe 2001), or transplanted seedlings into natural vegetation (Baraloto *et al.* 2005). All these studies show how potential for niche differentiation arises from differences between species in their responses to various combinations of environmental variables.

Seed size has been regarded as an important plant property since the pioneering studies of Salisbury (1942), but many studies on the ecological significance of seed size have been conducted in recent years because of its further role in plant community composition (Westoby *et al.*, 1996; Leishman *et al.*, 2000; Muller-Landau, 2003; Fenner & Thompson, 2005). It is well established that the relative growth rate of young seedlings is negatively correlated with seed size (Marañón & Grubb, 1993). However, larger-seeded species have been found to be superior competitors in dense stands. Smaller-seeded species can sometimes outcompete larger-seeded species only when seedlings are widely spaced (Weiner *et al.*, 2001). In general seedlings from larger-seeded species are more resistant to hazards (Leishman *et al.*, 2000), though exceptions have been found (Bloor & Grubb, 2003).

There have been relatively few experimental studies on seedlings performance of plants from alpine plant communities (Koerner, 2003), especially for forbs which are representational dominant species in disturbed and degraded meadows. Our study has been made on plants from alpine meadows on the Qinghai-Tibetan Plateau, where there is marked heterogeneity in the physical conditions considered at the scale of an individual seedling. The regimes of light and temperature are very complex, and therefore we set up this experiment in field with some plants in the open and others under neutral shade.

This paper studies two main themes: intraspecific performance variation of plants, and the dependence of seedling properties on seed size for these forbs species. The main objectives of this study were: (1) to test the effect of seed mass on seedling relative growth rate, allocation and functional morphology; (2) to test the impacts of light and nutrient availability on the same seedling properties; and (3) to discuss performance response to resources availability for seedling from the eight forbs with different seed size.

## Materials and Methods

**Study site:** The study was carried out at the Field Experiment Station of the State Key Laboratory of Arid Ecology of Lanzhou University, which is at the eastern end of the Tibetan Plateau (latitude 34°55'N, longitude 102°53'E). The mean altitude is about 3500 m, and the landscape consists of alpine meadow and subalpine meadow. The physiognomy of alpine meadows of the Qinghai-Tibetan Plateau is typical altiplano. Average annual temperature is 2.0°C, the lowest daily temperature averages -8.9°C concentrated in December, January, and February; the highest daily temperature averages 11.5°C concentrated in June, July, and August. The average precipitation of a year is 550 mm, concentrated in July, August, and September. The vegetation is typically an alpine meadow (Wu *et al.*, 2009). It consists mainly of arctic-alpine and Chinese Himalayan plants and is dominated by aboriginal constructive species, sedges (*Kobresia*), and grasses (e.g. *Agrostis*, *Elymus*, *Festuca*, *Poa*, *Stipa*). And, there are a wide variety of dicots (e.g. *Aconitum*, *Anemone*, *Gentiana*, *Ligularia*, *Pedicularis*, *Potentilla*, *Saussurea* and *Trollius*) and among these the genus *Anemone* and *Saussurea* are especially abundant. With the increasing of grazing disturbance and meadow degradation, many forbs species of the Asteraceae, the Ranunculaceae and the Fabaceae family were becoming current dominant species in meadow communities. So, we selected eight native forbs species (*Vicia sepium* L., *Anemone rivularis* Bur.et Franch., *Astragalus polycladus* Bur.et Franch., *Cremanthodium lineare* Maxim., *Trollius farreri* stapf, *Artemisia desertorum* Spreng., *Ranunculus tanguticus* var. *nematolobus*, and *Artemisia hedinii* Ostenf) which represent a wide range of seed size (in Table 1), to study their seedling performance response to variational light and nutrient availability. These seeds were collected from the Maqu country of Gannan County of Gansu Province of China in August-September 2003. The seeds were stored at +4°C until they were sown.

**Field experiment:** At our study site, the height of plants reached 40-60cm in autumn and the degree of shading at the soil surface reached 85% of natural daylight in sites dominated by graminoids. Shading by the canopy exceeded 90% at its seasonal maximum for partial grassland which was fertilized artificially. There was little seedling survival when the light availability was about 15% of natural daylight. The low light levels which permeate canopy severely

restricted seedling growth and recruitment (Wu *et al.*, 2006). The light conditions of moderately-grazed meadows and seriously-grazed meadows were approximately 25~50% and 50~90%. In addition, moderately- and seriously- grazing also decreased soil nutrient availability in alpine meadow (Wu *et al.*, 2009). So, we conducted four light regimes and three nutrients regimes (12 combined treatments) in this study. For the 100% daylight treatment (referred to as L100) no screen was used. For the other three treatments different densities of black plastic screening were used. We use two types of screenings with different density. The combinations of these two types of screen produced four levels of shadings and the no screen treatment, 100, 50, 25 and 12% of day light (referred as L100, L50, L25 and L12 respectively). The light intensity within 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,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) using the single sensor setting were taken from each light regime when it was fine day in the middle of June, 2004. We used the full-strength Hoagland solution as one nutrient treatment because it was easy to control (Meziane & Shipley, 1999). We changed nutrient availability by applying different strength of Hoagland solution, N0 (without nutrient), N50 (50% of full strength) and N100 (full strength). The nutrient solutions were added every five days when seedlings were emerged and 200 ml were sprinkled uniformly over each pot. N0 treatments received distilled water instead of nutrient solution. Preliminary germinations of all seeds were done in order to ensure sufficient seedlings for each species for following measurements. Seedlings were grown in plastic pots (40 cm × 40 cm × 50 cm) filled with fine-grained sand taken from the edge of the Yellow River, because we can take out the whole seedling from pots expediently. Sand was washed three times before using, the pH of the water-saturated sand was about 7.1. Seeds of all species were sown on the same day (20 April 2004). The experiments were undertaken for four months (to the last ten days of August 2004). In each plastic pot, 5 seeds were sown in a regular pattern to avoid competition among seedlings. 20 replicates of pots for each species in each treatment were set up with completely-randomized design in experimental plots. Apart from the normal rain, the seedlings were well watered during the all growth seasons and all treatments were given the same amount of water.

**Table 1. Summary of traits for eight herbaceous species and relative abundance in alpine meadows used in this field experiment. Seed masses are mean seed weight ( $\pm$  SE) per seed. Nomenclature and assignment to families follows Wu (1995). The last columns gives the relative abundances of mature individuals of each species in alpine meadow habitats, based on survey: VC, very common species; C, common. Species were ordered by the mean seed mass, and the initials used for them, their micro-habitats and relative abundances are given.**

Ab.	Species	Family	Seed mass (mg)	Relative abundance	Habitat
Vs	<i>Vicia sepium</i> L.	Fabaceae	19.6 $\pm$ 0.56	C	Dankness
Ar	<i>Anemone rivularis</i> Buch.–Ham.	Ranunculaceae	5.57 $\pm$ 0.15	VC	Dry and hollowness
Ap	<i>Astragalus polycladus</i> Bur.et Franch.	Fabaceae	1.42 $\pm$ 0.40	C	Dankness
Cl	<i>Cremanthodium lineare</i> Maxim.	Asteraceae	0.78 $\pm$ 0.03	C	Dry and hollowness
Tf	<i>Trollius farreri</i> Stapf	Ranunculaceae	0.48 $\pm$ 0.01	VC	Dry and hollowness
Ad	<i>Artemisia desertorum</i> Spreng	Asteraceae	0.25 $\pm$ 0.01	C	Dry and hollowness
Rt	<i>Ranunculus tanguticus</i> var. <i>nematolobus</i>	Ranunculaceae	0.17 $\pm$ 0.008	VC	Dry and hollowness
Ah	<i>Artemisia hedinii</i> Ostenf	Asteraceae	0.09 $\pm$ 0.005	C	Dry and hollowness

**Sampling:** All data for each species were measured at 20d, 40d, 60d and 80d after 50% of the seedlings emergence. On the basis of the number of seedlings emerged, we selected 3-5 pots per species per treatment at each harvest. From the 3-5 pots we harvested 15 seedlings to avoid the seedlings differences caused by the influence of belowground competitive or facilitative interactions, with identical growing stage (the seedlings have the same number of leaves and leaflets and the seedling size was similar). They were washed to remove the sand. The remaining pots were given the same treatment for later measurements. Leaf area (LA, mm<sup>2</sup>) was measured with a leaf area meter (LI-300A, Li-Cor, Lincoln, Nebraska, USA). The leaf area included the rachis for all species because the leaves were too small to be separated. Shoot height (mm) and rooting depth (mm) were measured for each seedling which was then oven-dried (70 °C) for 48h. The dry mass values were obtained for roots (Wr), stems (Ws) and leaves (Wl) with an electronic balance (precision 0.0001g). The individual seedling biomass (W) is the sum of Wr, Ws and Wl. Relative growth rate (RGR), specific leaf area (SLA), the leaf area ratio (LAR), the root to shoot height ratio (Lr/Ls), and the root to total seedling dry mass ratio (Wr/Ws) were also calculated by the following formulae:

$$\begin{aligned} \text{RGR} &= (\ln Wt_2 - \ln Wt_1) / (T_2 - T_1) \text{ (g g}^{-1}\text{d}^{-1}\text{)} & (1); \\ &\text{(where Wt is the whole seedling dry mass), Mean RGR of} \\ &\text{seedlings at 60 d used in this study.} \\ \text{SLA} &= \text{LA} / \text{WI} \text{ (mm}^2\text{/mg)} & (2); \\ \text{LAR} &= \text{LA} / \text{W} \text{ (mm}^2\text{/mg)} & (3); \\ \text{Wr/W} &= \text{Root dry mass/Dry mass of total individual seedling} & (4) \end{aligned}$$

**Statistical analyses:** The data were log-transformed before analyses to achieve normal distribution. All data of four harvest times were used as time repetitions. Effects of light and nutrient availability on the relationships between seed size and growth parameters were analyzed with ANCOVA of General Linear Model (GLM) and Type III sums of squares, with the light and nutrient availability as fixed factors and seed size and family as covariates to remove the variability caused by species relatedness. Other analyses were conducted with a two-factor ANOVA and a posteriori Tukey-Kramer HSD tests for significance ( $p < 0.05$ ). Correlations between seed mass and seedling growth traits were tested on the data pooling all nutrient and irradiance treatments. All data analyses were conducted with the SPSS software (SPSS for Windows, Version 13.0, Chicago, IL, USA).

## Results

**Seedling emergence:** We found that light availability ( $F = 2.951$ ,  $p < 0.05$ ) had a significant effect on seedling emergence time for eight species. These species needed a longer emergence time under shade conditions than high irradiance conditions. There was a non-significant negative relationship between seed size and seedling emergence time for all the species (Fig. 1). However, for three species within *Asteraceae* family, seedling emergence time was negatively associated with seed size under four light conditions ( $r = 0.75$ ,  $p < 0.0001$ ;  $r = 0.74$ ,  $p < 0.01$ ;  $r = 0.67$ ,  $p < 0.05$ ;  $r = 0.61$ ,  $p < 0.01$ , for L12, L25, L50 and L100 treatments, respectively). For three species

within *Ranunculaceae* family, significantly negative relationships between seedling emergence time and seed size were occurred under L12 ( $r = 0.35$ ,  $p < 0.05$ ) and L25 ( $r = 0.26$ ,  $p < 0.05$ , Fig. 2).

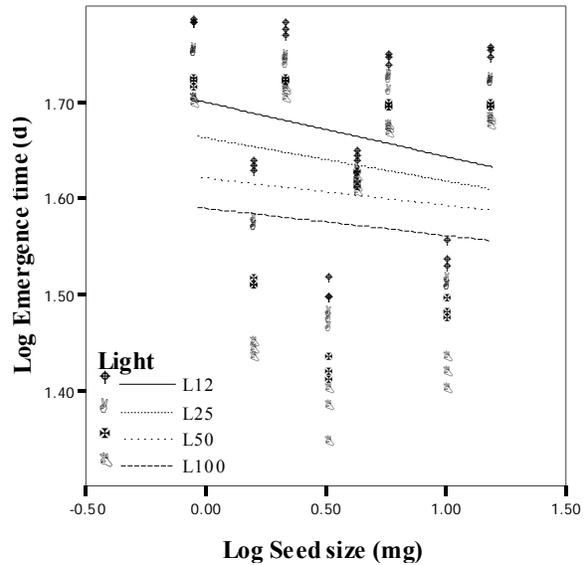


Fig. 1. Relationships between seed size and seedling emergence time of the eight study species under four irradiance conditions. Irradiances have four levels: L100, 100% of full daylight; L50, 50% of full daylight; L25, 25% of full daylight; L12, 12% of full daylight.

**Seedling biomass and allocation:** Seed size and nutrient availability both had significant effects and also showed interaction on seedling individual biomass (W,  $p < 0.0001$ ), shoot dry mass (Ws,  $p < 0.0001$ ) and root dry mass (Wr,  $p < 0.0001$ ). However, root to total seedling dry mass ratio (Wr/W) was only significantly affected by nutrient availability ( $p = 0.006$ , Table 2). We found a significant positive correlation between seedling biomass and seed size at N0 conditions ( $r = 0.84$ ,  $p < 0.0001$ ;  $r = 0.87$ ,  $p < 0.0001$ ;  $r = 0.80$ ,  $p < 0.0001$ ;  $r = 0.85$ ,  $p < 0.0001$ , for N0L100, N0L50, N0L25 and N0L12 treatments, respectively, Fig. 3), but not at N50 and N100 conditions. The maximum seedling biomass occurred under high light and nutrient availability (Appendix 1). By pooling all treatment data, shoot dry mass and root dry mass were both significantly positively correlated to seed size ( $r = 0.363$ ,  $p < 0.001$ ;  $r = 0.387$ ,  $p < 0.001$ , for Ws and Wr, respectively), and root to total seedling dry mass ratio (Wr/W) presented a non-significant positive relationship to seed size (Table 3). In addition, Wr/W showed an increasing trend with light availability, but a decreasing trend with nutrient availability ( $F = 6.426$ ,  $p < 0.01$ , Fig. 4).

**Seedling relative growth rate (RGR):** Results showed that seed size ( $F = 8.797$ ,  $p < 0.01$ ) and nutrient availability ( $F = 3.158$ ,  $p < 0.05$ ) both presented significant effects on RGR, but light did not (Table 2). RGR was significantly negatively correlated with seed size under N50 ( $r = 0.23$ ,  $p < 0.05$ ) and N100 ( $r = 0.28$ ,  $p < 0.05$ ), but not under N0 ( $r = 0.11$ ,  $p = 0.414$ ; Fig. 5). Meanwhile, high nutrient

availability increased RGR for these alpine species (Fig. 5). By pooling all treatment data, RGR was negatively correlated with seed size (mean Pearson's correlation coefficient  $r = -0.153$ ;  $p < 0.05$ , Table 3). Small-seeded species presented higher RGR. *Ranunculus tanguticus* var. *nematolobus*, *Artemisia hedinii* and *Artemisia desertorum* presented significant larger RGR than other five small-seeded species (Appendix 1). In addition, RGR were negatively correlated with Lr ( $r = -0.140$ ,  $p < 0.01$ ), Wr ( $r = -0.195$ ,  $p < 0.001$ ), Wr/W ( $r = -0.375$ ,  $p < 0.001$ ) and SLA ( $r = -0.116$ ,  $p < 0.05$ ), but positively correlated with LAR ( $r = 0.290$ ,  $p < 0.001$ ; Table 3).

**Morphological performances:** For seedling morphological performances (shoot height (Ls), root length (Lr), root to shoot height ratio (Lr/Ls), leaf

area (LA) and specific leaf area (SLA)) in our study, they were all significantly affected by seed size and nutrient availability and their interaction. Meanwhile, seed size was shown significant positive correlation with Ls ( $r = 0.517$ ,  $p < 0.001$ ), Lr ( $r = 0.484$ ,  $p < 0.001$ ), LA ( $r = 0.263$ ,  $p < 0.001$ ) and SLA ( $r = 0.209$ ,  $p < 0.001$ ), and significantly negatively correlated to Lr/Ls ( $r = -0.329$ ,  $p < 0.001$ ). However, leaf area ratio (LAR) showed a non-significantly negative relationship to seed size. LA was significantly negatively related to Lr/Ls ( $r = -0.593$ ,  $p < 0.001$ ), Wr/W ( $r = -0.321$ ,  $p < 0.001$ ) and SLA ( $r = -0.150$ ,  $p < 0.01$ ), and significantly positively related to LAR ( $r = 0.176$ ,  $p < 0.01$ ). Additionally, other performances also presented some interdependent correlations (Table 3).

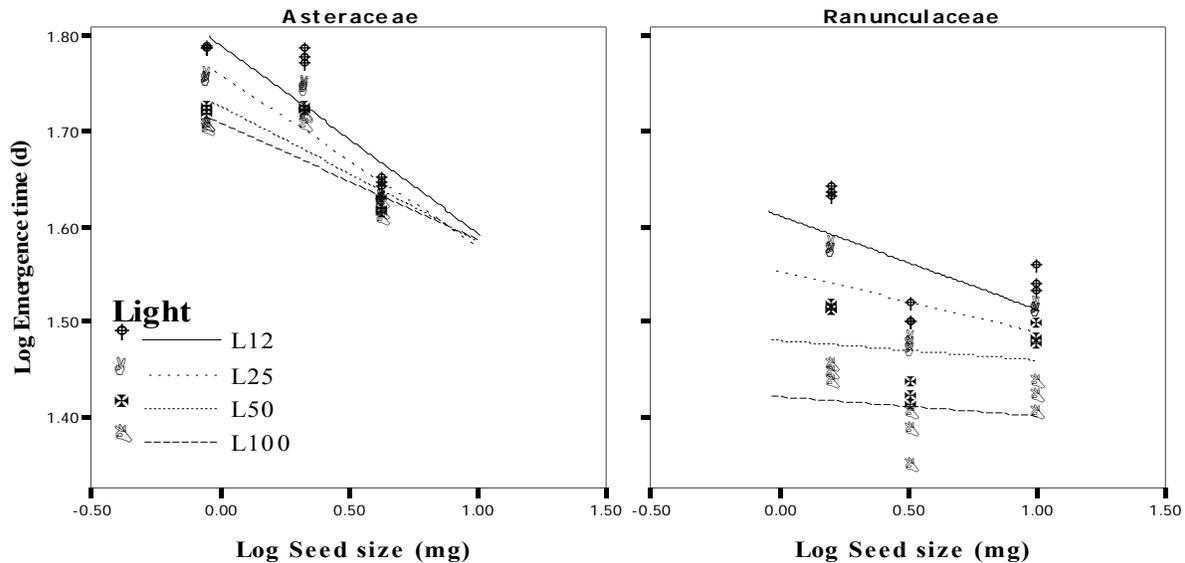


Fig. 2. Relationships between seed size and seedling emergence time within *Asteraceae* family (three species) and *Ranunculaceae* family (three species) under four irradiance conditions. Light treatments are same as Fig. 1.

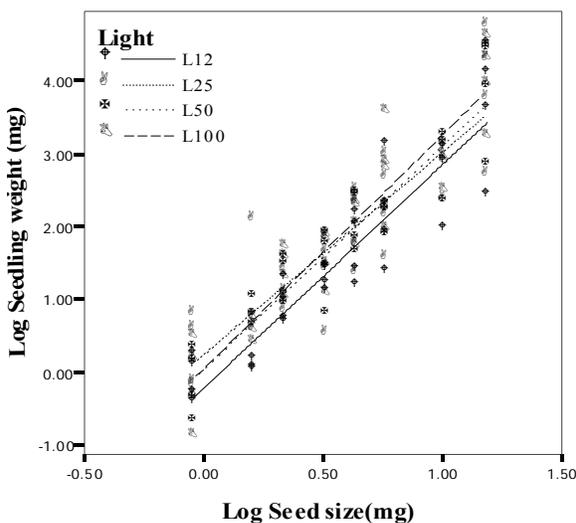


Fig. 3. Relationships between seed size and seedling weight under N0 (without nutrition) and four light treatments for the eight species studied at 60 d. Light treatments are the same as Fig. 1.

## Discussion

Our results showed that seed germination and seedling emergence were slower under shaded conditions. They revealed that light was an important factor which determined seed germination and seedling emergence time. Meanwhile, results contained significantly negative relationships between seed size and seedling emergence time within *Asteraceae* and *Ranunculaceae* families. It showed that small-seeded species will need a longer emergence time than large-seeded species within these families, because seed size is a useful general predictor of seedling emergence success (Bond *et al.*, 1999). Wu & Du (2008) had found that there were significant positive correlations between seed size and seed germination index for species within *Poaceae* family of the eastern Qinghai-Tibetan Plateau, China. So, we suggested that species with larger seeds had advantage in seed germination and seedling emergence than those with small seeds within family for these alpine species.

Successful establishment of seedlings depend critically on seed mass and its effects on early seedling

performance (Eriksson, 2005), especially on the seedling size (Fenner, 1983). Our results showed that the large-seeded species had an advantage in seedling size and this advantage will be more remarkable under nutrient scarcity condition for these alpine species, which were consistent with many other studies under shade conditions in other

regions (Fenner, 1983; Dolan 1984; Grubb *et al.*, 1996; Leishman *et al.*, 2000; Leishman & Murray, 2001; Coomes & Grubb, 2003; Moles & Westoby, 2004a, b; Murray *et al.*, 2005). Hence, it will unify that seedling mass was positively related to seed size among species within plant community of all over the world.

**Table 2. Response of growth parameters to light, nutrient availability, seed size and family (All data were log-transformed before analysis and were analyzed with ANCOVA, with light and nutrient availability as fixed factor and seed size and family as covariates).**

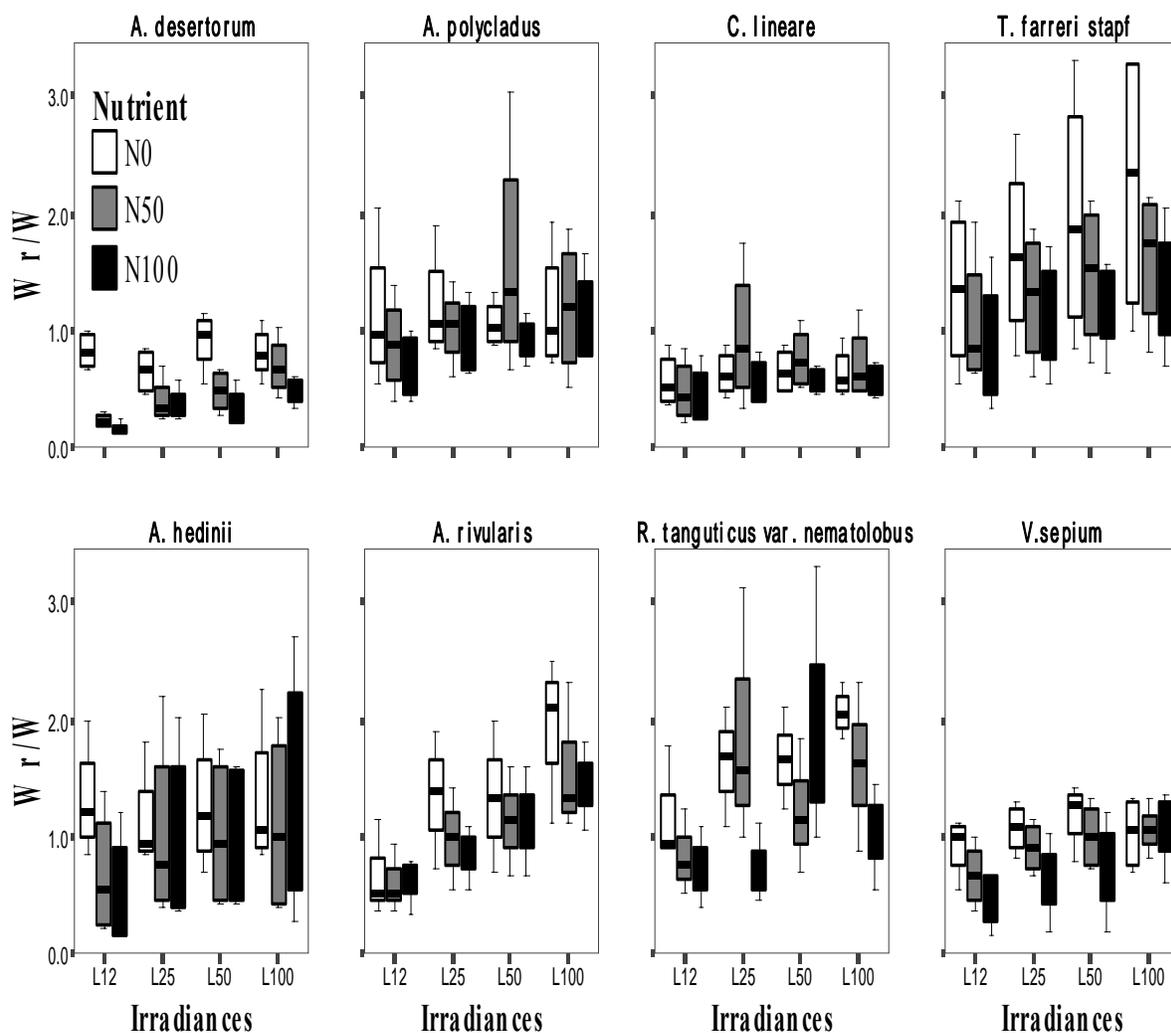
Parameters	Tests of between-subjects effects			F	Sig.
	Sources	df	Type III sum of squares		
W	Nutrient	2	30.659	93.406	<0.0001
	Seed size	1	15.933	97.082	<0.0001
	Nutrient* Seed size	2	15.502	47.230	<0.0001
	Error	336	55.144		
Wr	Nutrient	2	25.154	66.733	<0.0001
	Seed size	1	18.018	95.603	<0.0001
	Nutrient* Seed size	2	13.878	36.820	<0.0001
	Error	336	63.324		
Ws	Nutrient	2	35.011	117.012	<0.0001
	Seed size	1	15.503	103.628	<0.0001
	Nutrient* Seed size	2	16.970	56.714	<0.0001
	Error	336	50.267		
Wr/W	Nutrient	2	.292	5.190	0.006
	Error	336	9.462		
RGR	Nutrient	2	1.554	3.158	0.044
	Seed size	1	2.164	8.797	0.003
	Error	336	82.652		
Ls	Nutrient	2	8.120	89.932	<0.0001
	Seed size	1	11.201	248.087	<0.0001
	Nutrient* Seed size	2	3.546	39.273	<0.0001
	Error	336	15.170		
Lr	Nutrient	2	0.475	12.850	<0.0001
	Seed size	1	2.195	118.815	<0.0001
	Nutrient* Seed size	2	0.270	7.317	0.001
	Error	336	6.208		
Lr/Ls	Nutrient	2	4.715	50.463	<0.0001
	Seed size	1	3.478	74.458	<0.0001
	Nutrient* Seed size	2	1.860	19.911	<0.0001
	Error	336	15.697		
LA	Nutrient	2	26.293	79.878	<0.0001
	Seed size	1	5.471	33.243	<0.0001
	Nutrient* Seed size	2	11.474	34.858	<0.0001
	Error	309	50.855		
LAR	Nutrient	1	9.886	41.149	<0.0001
	Error	309	74.236		
SLA	Light	3	0.419	3.672	0.013
	Nutrient	2	0.318	4.176	0.016
	Seed size	1	0.678	17.819	<0.0001
	Nutrient* Seed size	2	0.380	4.998	0.007
	Error	309	11.761		

Notes: Ls, shoot height; Lr, root length; Wr, root dry mass; Ws, shoot dry mass; W, total individual seedling dry mass; RGR, relative growth rate; Wr/W, root to total seedling dry mass ratio; Lr/Ls, root to shoot height ratio; LAR, leaf area ratio; LA, leaf area; SLA, specific leaf area. Data were at 60 d seedlings of eight species. Significance was determined at  $P < 0.05$ , Tukey-Kramer HSD)

**Table 3. Pearson's correlation coefficients (r) for the relationships between all pairings of seed and seedling characteristics for 60-day seedlings of eight species. Correlations were performed considering the all nutrition and light intensity treatments under four harvesting times.**

	Seed size	RGR	Ls	Lr	W	Ws	Wr	LA	Lr/Ls	Wr/W	LAR
RGR	-0.153*										
Ls	0.517***	-0.012									
Lr	0.484***	-0.140**	0.483***								
W	0.371***	-0.078	0.799***	0.757***							
Ws	0.363***	0.005	0.863***	0.669***	0.969***						
Wr	0.387***	-0.195***	0.678***	0.793***	0.950***	0.890***					
LA	0.263***	0.031	0.829***	0.641***	0.905***	0.922***	0.795***				
Lr/Ls	-0.329***	-0.061	-0.881***	-0.011	-0.503***	-0.624***	-0.345***	-0.593***			
Wr/W	0.073	-0.375***	-0.337***	0.158**	-0.099	-0.191***	0.217***	-0.321***	0.471***		
LAR	-0.172	0.290***	0.055	-0.260***	-0.260***	-0.149**	-0.400***	0.176**	-0.197***	-0.472***	
SLA	0.209***	-0.116*	0.110*	0.049	0.208***	0.244***	0.304***	-0.150**	-0.097	0.326***	-0.821***

\*  $p < 0.05$ . \*\*  $p < 0.01$ . \*\*\*  $p < 0.001$



**Fig. 4.** Mean root mass to total mass ratio ( $W_r/W$ ,  $\pm$  SE) for the whole growth period in the eight studied species. Four light levels: L100, 100% of full daylight; L50, 50% of full daylight; L25, 25% of full daylight; L12, 12% of full daylight and three nutrient levels: N0, without nutrition; N50, 50% of full-strength Hoagland's nutrient solution; N100, 100% of full-strength Hoagland's nutrient solution.

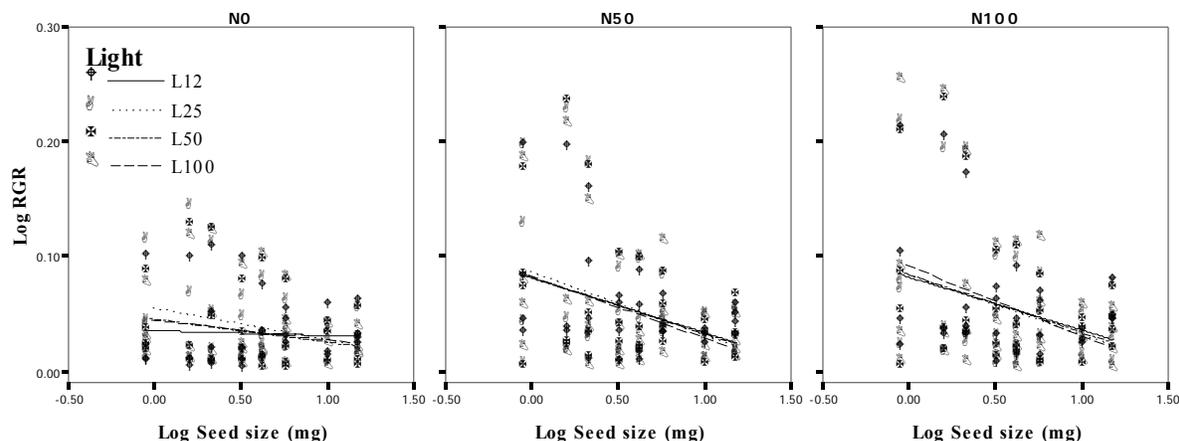


Fig. 5. Relationships between seed size and seedling relative growth rate (RGR,  $\text{mg mg}^{-1}\text{d}^{-1}$ ) for the eight studied species under twelve treatment conditions at 60 d. Light and nutrient treatments are same as Fig. 4.

Seedling life-history strategies (like relative growth rate (RGR), biomass allocation or other morphological traits) of different species were also affected by seed mass (Sultan, 2001; Coomes & Grubb, 2003; Suding *et al.*, 2003; Moles & Westoby, 2004a,b). Our results revealed that interspecific variation in seedlings RGR and biomass allocation was not only driven by the microhabitats (light and nutrient), but also by individual seed mass (Suding *et al.*, 2003). As mentioned, seedlings from the larger-seed species had a stronger advantage because of their larger initial seedling and height. Seedlings from larger-seeded species usually keep their performance advantage by larger biomass, height, leaf area and SLA. Seedlings from the smaller-seed species will be restrained in capturing light and other resources (Harper, 1977; Grubb, 1998). Our results showed that seedlings from smaller-seeded species had larger RGR, LAR, root to shoot height ratio and than those from larger-seeded species. Larger LAR increased effective area for light interception and net assimilation rate (Shanmuganathan & Benjamin, 1992) and high-proportional root length could allow the plant to gain much nutrient resources for smaller-seeded seedlings. So, all these revealed that seedlings from the smaller-seeded species increased root length and leaf area ratio to capture more resources. Our study found that light and nutrient availability all had significant effects on seedling morphological performance (shoot height, root length and root to shoot height ratio) for these species in alpine meadow. These indicated that seedlings from larger-seeded species and from smaller-seeded species could adopt different morphological strategy for their early growth. To varying degrees, seedlings that grow in resources-scarce habitats will adjust morphological performances in ways that tend to maximize photosynthetic efficiency (Poorter & Van der Werf, 1998). Response of functional traits on morphology and growth to environment usually was interpreted as a change in a plant's life-history strategy in response to resource availability (Miner *et al.*, 2005; Pigliucci, 2005).

In general, seed size and nutrient availability had the strongest effects on seedling performance in alpine meadows of the Qinghai-Tibetan Plateau. There was a consistency between other relations of seed mass and seedling ecology on the Qinghai-Tibetan Plateau when

compared with elsewhere in the world (Eriksson, 2005). Seedling performances were significantly prior-related to seed mass and nutrient availability than to light availability. Similarly, light and nutrient availability were all crucial limiting factors of seedlings recruitment for herbaceous plants in alpine meadows. To more fully understand the basis of species differences in ecological distribution, we should enhance the study on relationships of seedlings' life-history strategies and success in their recruitment in future, especially under the special habitats which had been disturbed in alpine meadow of the Qinghai-Tibetan Plateau.

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