



# Asian Journal of Plant Sciences

ISSN 1682-3974

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## Response of Morphological Plasticity of Three Herbaceous Seedlings to Light and Nutrition in the Qing-hai Tibetan Plateau

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**Abstract:** Three compositae herbaceous plants native to alpine meadows of the eastern Tibetan Plateau were examined for their morphological plasticity of seedling height, leaf area and Specific Leaf Area (SLA) in response to several light and nutrient levels. Present study indicated that the morphological growth traits of seedlings in alpine meadow were affected significantly by light and nutrition factors. These three species' seedlings height and leaf area responded negatively to light, but increased radiation decreased SLA. The larger-seed species had larger initial seedling height. Seedlings from the smaller-seed species had much greater ability to adapt different environment heterogeneity than did the bigger-seed species. Seedlings from the smaller-seed species had much morphological plasticity than seedlings from the larger-seed species to different environmental heterogeneity in alpine meadow community. Environment conditions had a significant effect on the seedling growth, which was the phylogenetic cause; but seed mass also had a significant influence on seedlings' growth, which also could affect the alpine meadow regeneration dynamics in the Qing-hai Tibetan Plateau.

**Key words:** Leaf area, plant height, specific leaf area, seedling, light, nutrition, alpine meadow

### INTRODUCTION

Phenotypic plasticity is widespread in morphological and life-historical traits. It is now clear that a wide diversity of organisms express phenotypic plasticity in response to biotic and abiotic aspects of their environments (Miner *et al.*, 2005). Plasticity has also been suggested as a potentially important mechanism facilitating macroevolution (West-Eberhard, 2003). The study of phenotypic plasticity focused on shade avoidance traits in the plant. They found that there was a high degree of microenvironmental variation in selection coefficients with the shade avoiding phenotype only being advantageous at some microsites. These plastic responses include changes in behavior, physiology, morphology, growth, life history and demography and can be expressed either within the lifespan of a single individual or across generations (Agrawal *et al.*, 1999; Young *et al.*, 2003; Miner *et al.*, 2005). The morphological plasticity might lead to the maintenance of phenotypic plasticity in response to changes in light (Pigliucci, 2005). Plasticity in morphology usually was understood as phenotypic accommodation—a change in a plant's

life-history strategy in response to the resources availability of environment. Pigliucci (2005) suggests that adaptive phenotypic plasticity occurs in natural populations and average differences among environments across genotypes. The recognition that plasticity can be adaptive has stimulated a wealth of studies on how plasticity alters interactions between individual organisms and their environments (Sultan, 2000). Plants alter the growth and structure of roots in response to different concentrations of nutrients, which maximizes nutrient foraging in patchy soils. This response increases the capture of essential nutrients and affects competitive interactions among plant species (Hodge, 2004). Many studies have shown that plasticity affects direct interactions between individuals and their biotic (e.g., competition) and abiotic (e.g., light and nutrition) environments in a variety of ways and in a wide range of taxa (Sultan, 2000; Pigliucci, 2001).

The change in its plasticity by altering the height and the evolution of growth strategy rather than the shape in species is possible. Research indicated that the variation of light intensity affected significantly the seedling survival and growth (Broncano *et al.*, 1998). The effects

of light availability on plant growth differed greatly among species of contrasting shade tolerance. Some species had morphological plasticity to facilitate capturing light in shade. For many plants, full sunlight was not required to maximize growth. Any herbaceous plants needed only about 10% of full sunlight to reach a state of growth where photosynthesis exceeds respiration and reach light saturation at 50% (C3 plants) and 85% (C4 plants) of full sunlight, respectively. Rees *et al.* (2001) suggested that plant traits variation among species had important implications for ecosystem processes. Species difference in seedling survival in different shade may depend on both seed mass and other growth parameters, Light and nutrient availability were the crucial factors during every stage of plant growth, especially in the earlier period of growth-seedling growth. Seedlings had greater plasticity than adults to the variation of light and nutrient availability. We usually consider that seedling height, Specific Leaf Area (SLA) and leaf morphology are an index of plant growth potential and key traits in relation to resource availability utilization. The plastic responses to heterogeneous environmental conditions are one of the most common phenomena characterizing the plant. The vertical foliage distribution also strongly affected physiological processes such as photosynthesis and individual plant growth (Xiao and Ceulemans, 2004). The leaf area of seedlings showed a tendency of decline with lower soil fertility (Ashton and Hall, 1992; Chapin, 1980; Dolph and Dilcher, 1980). Research indicated potentially important interactions among light, nutrition and species that could influence regeneration dynamics (Walters and Reich, 2000). But the research about the seed mass and seedling growth parameters (e.g., plant height, leaf area, specific leaf area etc.) in different environment conditions (light and nutrition availability) were few, especially in alpine meadow of Qing-hai Tibetan Plateau.

Seed mass as an intrinsic genetic aspect affects many aspects of plant ecology (Moles *et al.*, 2005), especially during the course of seedling growth. It was a central feature of a species' life history and ecology (Harper *et al.*, 1970). Ecologists interested in seed mass have generally contrasted functional groups of plants, but recently some focused on explaining the large range of seed mass found within a functional group. They advanced the idea of seed number-seedling survival tradeoff theory, which suggested that smaller-seeded species were superior colonizers and larger-seeded species were superior competitors in transitory seedling stages (Coomes and Grubb, 2003). Many researchers have concluded that the seedling from the larger-seed species has the stronger tolerance of hazards and pressures during the seedling establishment.

The alpine meadow is a unique natural landscape and an important grassland resource; not found any where else on earth. But in recent years, with the changing of global climate, the alpine meadows have presented seriously degeneration. Regional environment change is not suitable for the growth of some species in alpine meadow. Researches indicated that climate change appears to accelerate alpine meadow degeneration. The degradation of alpine meadow has increased peoples' awareness of the research of the alpine meadow. The degradation and renewing mechanism of alpine meadow is not clear, but we know the seedlings recruitment is a key process in alpine meadow vegetation succession.

We selected three widespread composite species in alpine meadow to conduct this field experiment to determine: (1) how seedlings of alpine meadow response to the light and nutrition by the plasticity; (2) what factors affect the morphological plasticity studied; (3) if seedlings from the smaller-seed species have any advantages in their adaptation to the variational light and nutrition in the alpine meadow community.

## MATERIALS AND METHODS

**Study site:** Three native species (Table 1) were collected from the Ganan state, Gansu Province, in China, which is located in the north-east of the Qinghai Tibetan plateau (101°53' E, 35°58' N). The altitude is approximately 3500 m and the climate is humid-alpine, with a mean annual rainfall of 620 mm which is mainly distributed in summer. Mean annual temperature is 1.2°C with -10.7°C in January and 11.7°C in July and with average annual frost days of more than 270d. The vegetation belongs to typical sub-alpine meadow (Du *et al.*, 1995).

**Study species:** These species (*Cremanthodium lineare* Maxim, *Artemisia desertorum* Spreng, *Artemisia hedinii* Ostenf) can be found in almost all of the regions of Ganan and are well-known species. From June to October 2003, seeds were collected in different populations which were big enough to supply abundant mature seeds. In this study, a seed is defined as the whole diaspore and the seed size refers to the quantity of achene reserve, which is similar to previous studies of seed size (Jurado *et al.*, 1991), measured as the seed dry weight (Fenner, 1983). We weighed 100 seeds from pooled

Table 1: Mean seed weight (SW) ( $\pm$ SE) per hundred seeds of studied herbaceous species

Ab	Species	Seed weight per 100 seeds (mg)	Family
C1	<i>Cremanthodium lineare</i> Maxim.	77.83 $\pm$ 2.67	Compositae
Ad	<i>Artemisia desertorum</i> Spreng	25.30 $\pm$ 1.06	Compositae
Ah	<i>Artemisia hedinii</i> Ostenf.	9.07 $\pm$ 0.54	Compositae

collections three times for each species and then took the mean weights per hundred seeds (Table 1).

**Field experiment:** The seeds of these species were sown in plastic pots (40×40×50 cm) at the same time. The plots were filled with washed sand (no nutrient matter). In each plastic pot were uniformly sown 10 seeds. Every species in each treatment were repeated 10 plots. Each species were sown in one of twelve treatment environments. Apart from normal rain, the seedlings were well watered during the all growth seasons. All treatment were meted the same water.

This experiment controlled principally irradiance, nutrient treatments and divided them into twelve treatment conditions: L1F0, L1N1, L1N2, L2N0, L2N1, L2N2, L3N0, L3N1, L3N2, L4N0, L4N1 and L4N2. Irradiance treatments included four levels: L1, 100% of full sunlight; L2, 50% of full sunlight; L3, 25% of full sunlight; L4, 12% of full sunlight. The light intensity conditions were controlled with different-density black plastic screening. Three nutrient treatments were: F0, without nutrition; F1, 50% of full-strength Hoagland's nutrient solution; F2, 100% of full-strength Hoagland's nutrient solution. The nutrient solutions were added once a day. F0 treatments were added the same water. These treatments were being at all times after sowing. Others were in natural field environments.

**Measurements:** The three growth parameters used in this study were determined by formulae as follows:

SLA Special Leaf Area:  $SLA = 1 \text{ g (leaf area/leaf dry weight) (cm}^2 \text{ g}^{-1}\text{)}$ ;

The leaf area was the total leaf area of a single seedling ( $\text{mm}^2$ );

The plant height was the whole length of the seedling (cm).

**Statistical analyses:** The data was analyzed statistically with the SPSS 11.0 package and ANOVA analysis was done. Differences in individual seedling whole height, leaf area and SLA in different treatments (light intensity, nutrition) were evaluated with analysis of variance and F-test to test the difference between means ( $p = 0.01$ ).

### RESULTS

These plastic responses in present study include chiefly change in morphology. The seedling plasticity altered ecological patterns and traits of seedling at the level of individuals in alpine meadow of Qing-hai Tibetan Plateau.

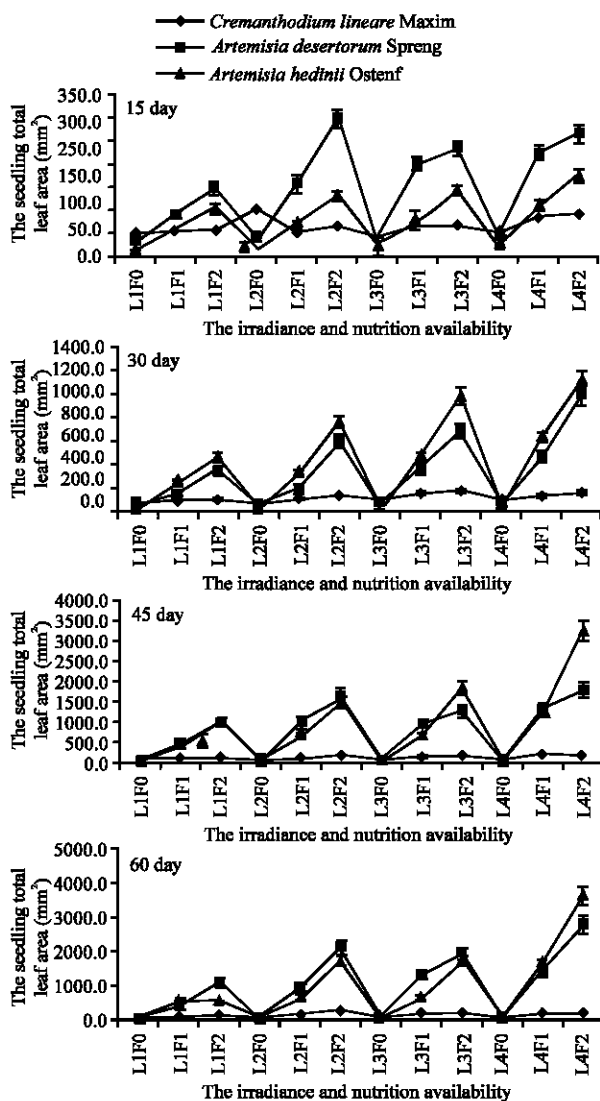


Fig. 1: The seedling individual total leaf area of *Cremanthodium lineare* Maxim, *Artemisia desertorum* Spreng and *Artemisia hedinii* Ostenf under different treatments for 15, 30, 45 and 60 day

**Leaf area:** The individual seedling leaf area was affected significantly by different light (ANOVA,  $F = 12.28$ ,  $p < 0.001$ ), nutrient availability (ANOVA,  $F = 12.28$ ,  $p < 0.001$ ), growth times (ANOVA,  $F = 31.20$ ,  $p < 0.001$ ) and species (ANOVA,  $F = 12.28$ ,  $p < 0.001$ ) (Table 3). The seedling total leaf area increased with nutrition availability and the reduced with light (Fig. 1, 4 and 7). There was a significant positive correlation between leaf area, growth time and nutrient availability; however, there was a negative correlation between leaf area and light. Seedlings had larger leaf area in lower light (Fig. 1, 4 and 7).

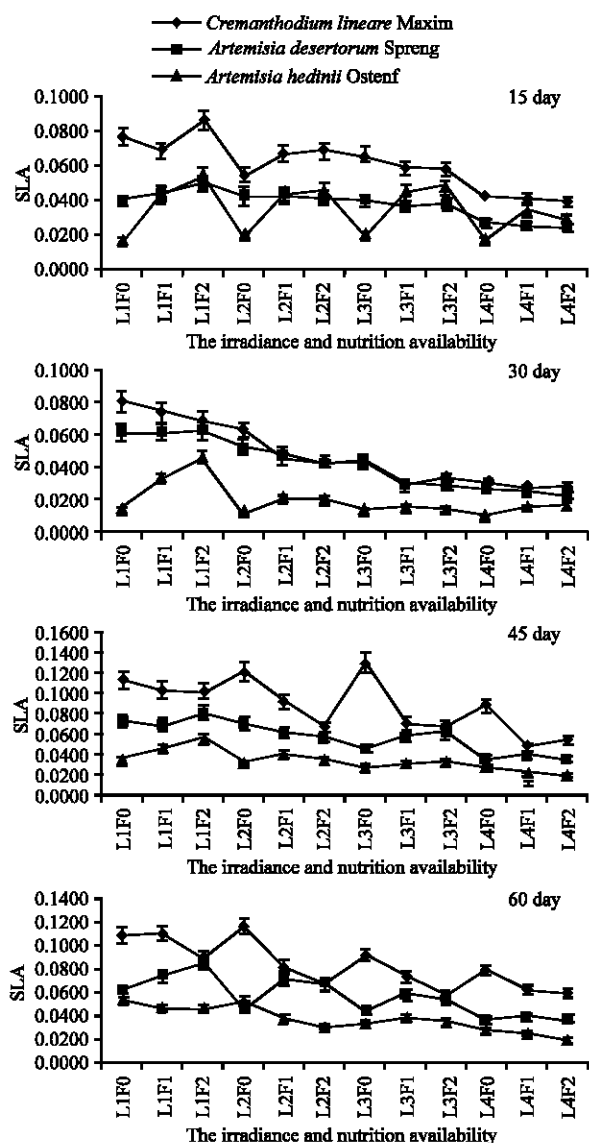


Fig. 2: The seedling specific leaf area of *Cremanthodium lineare* Maxim, *Artemisia desertorum* Spreng and *Artemisia hedinii* Ostenf under different treatments for 15, 30, 45 and 60 day

The correlation between seed mass and seedling total leaf area was the maximum in the 30 d, it reduced when the seedling grew in succession (Table 2). In the 15 d, the *Cremanthodium lineare* Maxim seedling had significant variety in different light and nutrition availability, but in 30-60 d the variety were little, however, the *Artemisia desertorum* Spreng and *Artemisia hedinii* Ostenf seedlings had significant response to the light and nutrition availability all along (Fig. 1, 4 and 7).

The larger-seed species (*Cremanthodium lineare* Maxim.) had a smaller leaf area, but the smaller-seed

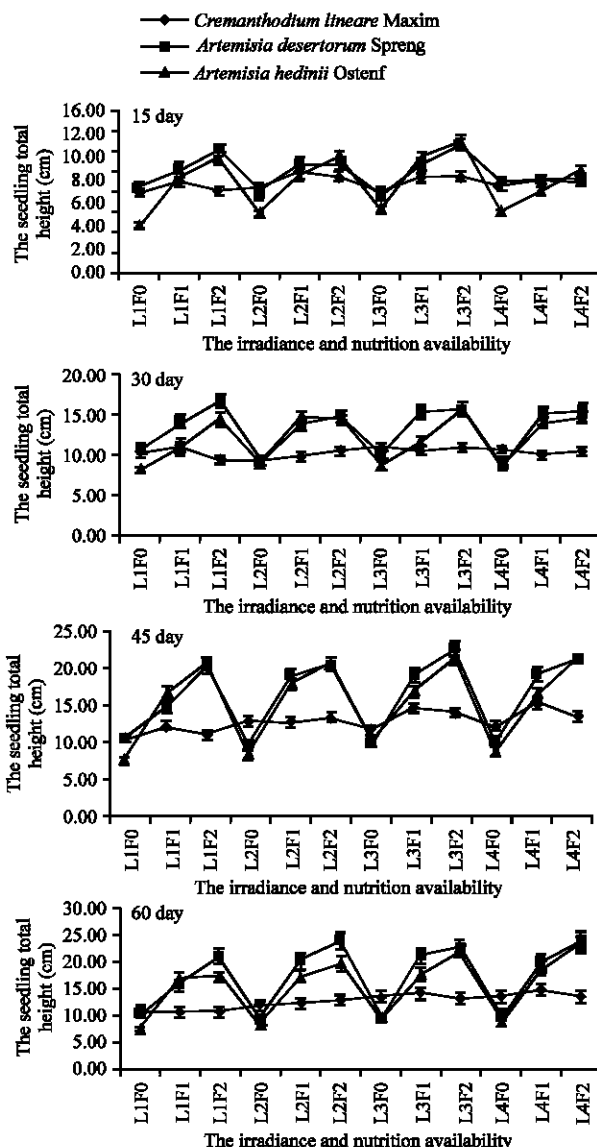


Fig. 3: The seedling total height of *Cremanthodium lineare* Maxim, *Artemisia desertorum* Spreng and *Artemisia hedinii* Ostenf under different treatments for 15, 30, 45 and 60 day

species (*Artemisia desertorum* Spreng and *Artemisia hedinii* Ostenf) had a larger leaf area. The larger-seed species (*Cremanthodium lineare* Maxim.) had little change in different irradiance and nutrition availability. However, the smaller-seed species *Artemisia desertorum* Spreng and *Artemisia hedinii* Ostenf had significant variety (Fig. 1).

**Specific leaf area:** The SLA of the three species seedlings were affected significantly by different light (ANOVA,  $F = 31.16, p < 0.001$ ), growth times (ANOVA,  $F = 20.23,$

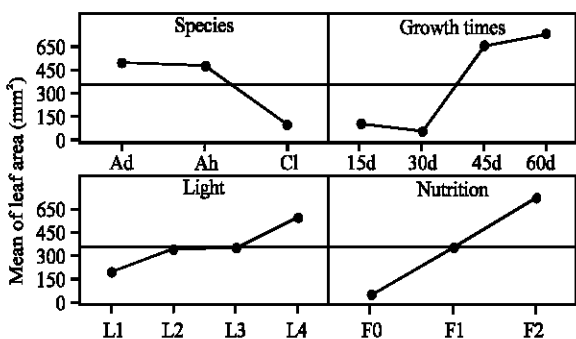


Fig. 4: The main effects plot of different factors on individual seedling leaf area

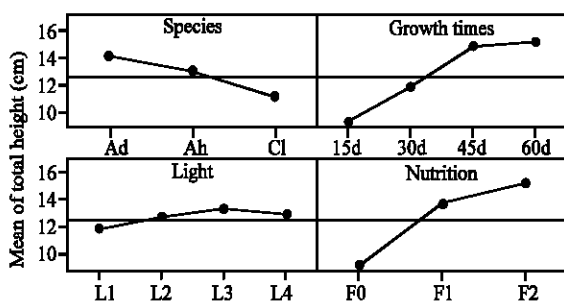


Fig. 5: The main effects plot of different factors on seedling total height

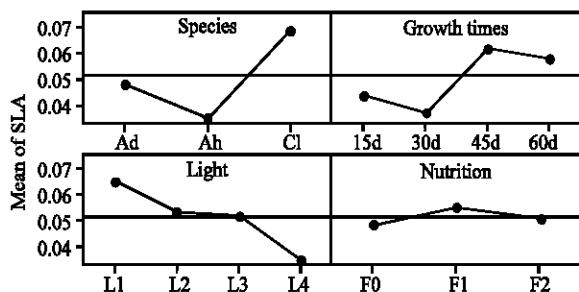


Fig. 6: The main effects plot of different factors on seedling Specific Leaf Area (SLA)

$p < 0.001$ ) and species (ANOVA,  $F = 4.91$ ,  $p < 0.001$ ) but nutrient availability (ANOVA,  $F = 1.35$ ,  $p = 0.260$ ) (Table 3). The SLA decreased with shade and attained a maximum under medium nutrition condition (Fig. 2 and 6). The SLA increased with nutrition under natural light condition but decreased with nutrition under deep shade condition. The SLA increased firstly and decreased latterly under medium shade condition (Fig. 9).

The SLA of *Artemisia hedinii* Ostenf seedlings was increased with the enhanced nutrition availability in 15-45 d (ANOVA,  $F = 4.91$ ,  $p = 0.002$ ) (Table 3). The differences were obvious, especially in the 15 d, but diminished with the increase of nutrition availability in 60 d. The smaller-seed species (*Artemisia hedinii*

Table 2: Pearson's coefficients of correlation ( $r$ ) for relationships (with significant  $p < 0.05$  coefficients in bold) between all pairings of seed and seedling attributes for 15d, 30d, 45d, 60d seedlings of three species. Correlations were performed considering the all nutrition and light intensity treatments

		Seed mass			
15 day	Leaf area	0.210	Leaf area		
	Plant height	0.802	0.475	Plant height	
	SLA	0.637	0.524	0.795	SLA
		Seed mass			
30 day	Leaf area	0.739	Leaf area		
	Plant height	0.898	0.670	Plant height	
	SLA	0.474	0.553	0.668	SLA
		Seed mass			
45 day	Leaf area	0.583	Leaf area		
	Plant height	0.794	0.670	Plant height	
	SLA	0.372	0.805	0.615	SLA
		Seed mass			
60 day	Leaf area	0.497	Leaf area		
	Plant height	0.760	0.824	Plant height	
	SLA	0.315	0.719	0.577	SLA

Note: Seed mass is the seed weight of hundred seeds, Leaf area is the total leaf area of a seedling, Plant height is the whole seedling height, SLA is the specific leaf area

Ostenf) had lower SLA than the larger-seed species (*Cremanthodium lineare* Maxim) (ANOVA,  $F = 20.32$ ,  $p < 0.001$ ) (Fig. 2.). The correlation between seed mass and seedling specific leaf area were reduced along with seedling growth (Table 2).

**Plant height:** The total plant height was affected significantly by different light (ANOVA,  $F = 18.57$ ,  $p < 0.001$ ), nutrient availability (ANOVA,  $F = 60.79$ ,  $p < 0.001$ ), growth times (ANOVA,  $F = 74.23$ ,  $p < 0.001$ ) and species (ANOVA,  $F = 113.56$ ,  $p < 0.001$ ) (Table 3). The seedling height increased with shade a certain extent. The seedling reached a relative maximum height under medium light availability (Fig. 3, 5 and 8). Seedlings have a significant positive relationship with nutrition availability (Fig. 5 and 8).

The correlation between seed mass and seedling height gradually fell with growth time (Table 2). The effects of seed mass on seedling height were chiefly exhibited in the early stage of seedling growth. The larger-seed species had larger initial seedling height determined by the different species phylogenetic evolution levels. So the *Cremanthodium lineare* Maxim seedlings were higher than seedlings of *Artemisia desertorum* Spreng and *Artemisia hedinii* Ostenf. The seedling height of *Cremanthodium lineare* Maxim had little variety to the nutrition availability relatively than *Artemisia desertorum* Spreng and *Artemisia hedinii* Ostenf. The seedlings from the smaller-seed species (*Artemisia desertorum* Spreng and *Artemisia hedinii* Ostenf.) had significant response to the nutrition availability (Fig. 5 and 8).

Table 3: Four-ways (light, nutrition and species) ANOVA summary of all effects on the growth of total height, leaf area, and SLA during the seedling growth stage

	Light		Fertilization		Species		Time	
	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value	F-ratio	p-value
Total height	18.57	0.000	60.79	0.000	113.56	0.000	74.23	0.000
Leaf area	12.28	0.000	12.28	0.000	12.28	0.000	31.20	0.000
SLA	31.16	0.000	1.35	0.260	20.32	0.000	4.91	0.002

Notes: Data are means ( $\pm$ SE) for seedling in different factors, Significance was determined at  $p < 0.01$ , Tukey-Kramer HSD)

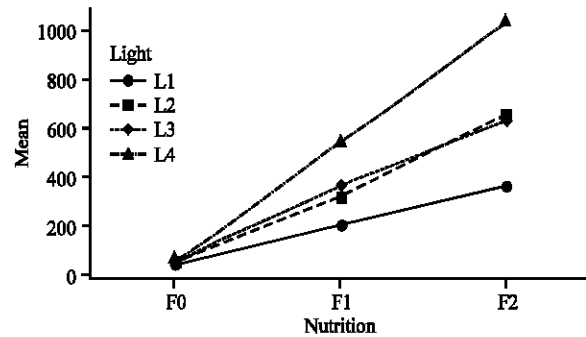


Fig. 7: The interaction effects plot of different factors on individual seedling leaf area ( $\text{mm}^2$ )

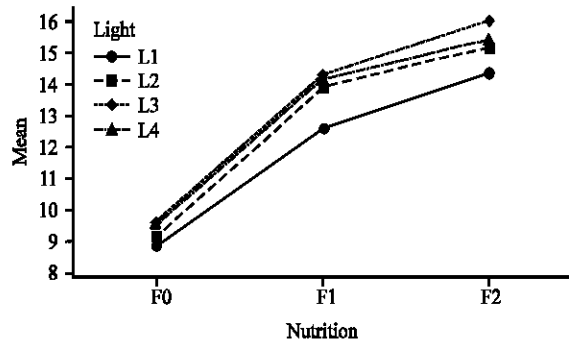


Fig. 8: The interaction effects plot of different factors on seedling total height (cm)

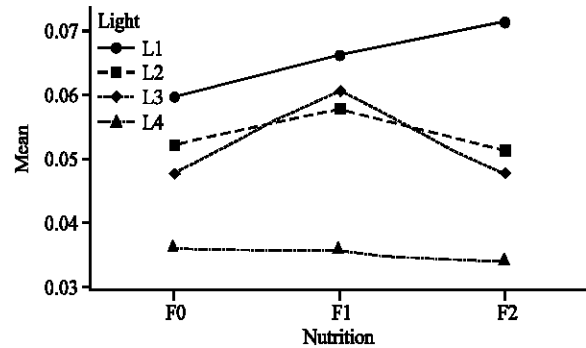


Fig. 9: The interaction effects plot of different factors on the seedling Specific Leaf Area (SLA)

## DISCUSSION

In alpine meadow of the Qinghai Tibetan Plateau, grassland is an important component of ecosystem which had played a major role in sustainable management of the alpine meadows of the Qinghai Tibet. The seedlings growth depends on the food reserves in the seed, the further seedling growth will be determined by the growing conditions, which reflect the adaptability of the seedlings. Species vary in their response to these conditions. Most of the morphological traits associated with the size of the plant parts and the timing of growth may vary according to environmental conditions.

In the area seriously damaged by rodents, useful grass has difficulty in growing; however, poisonous weeds have a positive effect on the recruitment of seedlings in a certain extent. We concluded that poisonous weeds produced stated shade which was useful for seedlings recruitments of some species through present experiment. So we could try adding seeds of useful grass in the grassland in which poisonous weeds are growing in a certain extent, which may accelerate benign succession of alpine meadow. The other way round, seedlings recruitment are difficult in the grassland which was bare damaged or full of poisonous weeds. Therefore, quantificational poisonous weeds could be seen as important resources for the seedlings recruitment in some grassland.

The different growth traits of species may chiefly be decided by their genetic phylogenetic evolution levels. Many studies have shown that plasticity affects direct interactions between individuals and their biotic (e.g., competition) and abiotic (e.g., light and nutrition) environments in a variety of ways and in a wide range of taxa (Sultan, 2000; Pigliucci, 2001). Potential height and morphological traits are important aspects of the ecology of plant species (Westoby *et al.*, 2002; Falster *et al.*, 2003). Some discussion of limits to height proceeds as if natural selection will inevitably drive plants to the tallest height that can be achieved in an environment (Ryan and Yoder, 1997).

These traits of seedling such as Specific Leaf Area (SLA) that modify the shading power of seedling individuals at a fixed height (Falster and Wesoby, 2003). The benefit of height is pre-emptive access to light; this competitive advantage depends on relative rather than absolute height. So the initial height of a seedling has a competitive advantage for its establishment achievement. Seedlings attained the light resource by increasing the height and leaf area in shade. Under the same nutrition levels, the seedling height and leaf area had an increase in the lower irradiance, especially under the enough nutrition conditions; the seedlings would transfer much biomass to the height for gaining the light resource to grow. Robakowski *et al.* (2003) concluded that seedling height and total leaf area responded positively to light, but increased radiation decreased LAR, SLA. Present study indicated these three species' seedlings height and leaf area responded negatively to light, the SLA variation was consistent with the result of Robakowski *et al.* (2003).

The seedlings from the larger-seed species had advantages of initial seedling height and initial seedling biomass (Coomes and Grubb, 2003), but had little adaptational ability to different micro-conditions and could not respond to the variety of growth surroundings. The seedlings from the smaller-seed species had flexible growth traits, which had some advantages for growth. The seedlings from larger-seed species (*Cremanthodium lineare* Maxim) had little response to the variational light and nutrition availability than seedlings from smaller-seed species. The smaller-seed species had no advantage on germination and initial seedling biomass, but they had a larger leaf area and plastic response to environment to increase their competition ability. The smaller-seed species were preponderant on being seasoned with different environmental conditions than the larger-seed species, which have a preponderant accommodation to the environment heterogeneity. They could transfer their biomass to leaf to adapt to the different micro-conditions. The smaller-seed seedlings adapted a different growth strategy from the larger-seed seedling. The smaller-seed seedlings increased the specific leaf area to improve their competition ability under abundant nutrition resources. The smaller-seed species seedlings had much stronger adaptation ability in different environment heterogeneity.

Ecologists have understood that there is a trade-off between seed size and seed number (Smith and Fretwell, 1974) and between seed number and seedling survival (Coomes and Grubb, 2003). From the above-mentioned discussion, we can reflect that seedling from larger-seed species and smaller-seed species have different growth strategies in these growth traits. We could think that there were a trade-off between seed mass and some seedling

growth traits, which may be the result of the species phylogenetic evolution and natural selection in special environment. The seedlings from larger-seed species had initial advantages of seedling biomass and height (Coomes and Grubb, 2003) and could suffer many hazard in the course of establishment (Moles *et al.*, 2005), but the seedling from smaller-seed species adopted different and flexible growth strategies which helped to hold some growth advantages.

Present study indicated that the morphological growth traits of seedlings in alpine meadow were affected significantly by the abiotic factors (light and nutrition) besides biologic factors. These biologic factors have an important effect on the alpine meadow succession. These species have the ability of grow well in a variety of nutrient availability and under different kinds of environmental conditions. The species studied here showed that seedlings from the smaller-seed species had much stronger tolerance to different environment heterogeneity, which could adapt the micro-environment by the plastic changes of some morphological growth traits. We concluded that the seedlings from the smaller-seed species had much morphological plasticity than seedlings from the larger-seed species in alpine meadow community of the Qinghai Tibet plateau. Some growth traits were determined by the phylogenetic characteristics, but natural selection was a more important role in the process of the species evolution. There are special climates in the alpine meadow of the Qinghai Tibet, which formed the severe selection pressures on local native plant species growth. These relationships between seed mass, seedling growth, seedling establishment, special climate environment and alpine meadow regeneration dynamics should be studied thoroughly. The key factors which controlled alpine meadow degeneration succession should be searched out.

#### ACKNOWLEDGMENTS

This research was funded by the Key Project of Natural Science Foundation of China (90202009) and Project of Natural Science Foundation of China (30470307).

#### REFERENCES

- Agrawal, A.A. *et al.*, 1999. Transgenerational induction of defences in plants and animals. *Nature*, 401: 60-63.
- Angela, T. Moles *et al.*, 2005. A brief history of seed size. *Sciences*, 307: 576-580.



- Ashton, P.S. and P. Hall, 1992. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *J. Ecol.*, 80: 459-481.
- Broncano, M.J., M. Riba and J. Retana, 1998. Seed germination and seedling performance of two Mediterranean tree species, holm oak (*Quercus ilex* L.) and Aleppo pine (*Pinus halepensis* Mill.): A multifactor experimental approach. *Plant Ecol.*, 138: 17-26.
- Chapin, F.S., 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.*, 11: 233-260.
- Chun-Wang, Xiao and R. Ceulemans, 2004. Allometric relationships for below-and aboveground biomass of young Scots pines. *For. Ecol. Manage.*, 203: 177-186.
- Coomes, D.A. and P.J. Grubb, 2003. Colonization, tolerance, competition and seed-size variation within functional groups. *Trends Ecol. Evolu.*, 18: 283-291.
- Dolph, G.E. and D.L. Dilcher, 1980. Variation in leaf size with respect to climate in the tropics of the Western Hemisphere. *Bulletin of the Torrey Botanical Club*, 107: 154-162.
- Du, G.Z. and G., Wang, 1995. Succession and qualitative change of artificial grassland of Gan Nan Sub-Alpine Meadow. *Acta Bot. Sin.*, 37: 306-313.
- Falster, D.S. and M. Westoby, 2003. Plant height and evolutionary games. *Trends Ecol. Evolu.*, 18: 337-343.
- Fenner, M., 1983. Relationships between seed weight, ash content and seedling growth in twenty-four species of compositae. *New Phytol.*, 95: 697-706.
- Harper, J.L., P.H. Lovell and K.G. Moore, 1970. The shapes and sizes of seeds. *Ann. Rev. Ecol. Syst.*, 1: 327-356.
- Hodge, A., 2004. The plastic plant: Root responses to heterogeneous supplies of nutrients. *New Phytol.*, 162: 9-24.
- Jurado, E., M. Westoby and D. Nelson, 1991. Diaspore weight, dispersal, growth form and perenniality of central Australian plants. *J. Ecol.*, 79: 811-826.
- Mark, A., Davis, Keith J. Wrage and Peter B. Reich *et al.*, 1999. Survival, growth and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. *Plant Ecol.*, 145: 341-350.
- Miner, B.G., S.E. Sultan and S.G. Morgan *et al.*, 2005. Ecological consequences of phenotypic plasticity. *Trends Ecol. Evolu.*, 20: 685-692.
- Pigliucci, M., 2001. *Phenotypic Plasticity: Beyond Nature and Nurture*, Johns Hopkins University Press.
- Pigliucci, M., 2005. Evolution of phenotypic plasticity: where are we going now? *Trends Ecol. Evolu.*, 20: 481-486.
- Robakowski, P., P. Montpied and E. Dreyer, 2003. Plasticity of morphological and physiological traits in response to different levels of irradiance in seedling of silver fir (*Abies alba* Mill.). *Trees*, 17: 431-441.
- Rees, M. *et al.*, 2001. Long-term studies of vegetation dynamics. *Sciences*, 293: 650-655.
- Ryan, M.G. and B.J. Yoder, 1997. Hydraulic limits to tree height and tree growth. *Bioscience*, 47: 235-242.
- Smith, C.C. and S.D. Fretwell, 1974. The optimal balance between the size and number of offspring. *Am. Natu.*, 136: 154-166.
- Sultan, S.E., 2000. Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci.*, 5: 537-542.
- Walter, M.B. and P.B. Reich, 2000. Seed size, nitrogen supply and growth rate affect tree seedling survival in deep shade. *Ecology*, 81: 1887-1901.
- Westoby, M. *et al.*, 2002. Plant ecological strategies: some leading dimensions of variation between species. *Ann. Rev. Ecol. Syst.*, 33: 125-159
- West-Eberhard, M.J., 2003. *Developmental Plasticity and Evolution*. Oxford University Press.
- Young, T.P. *et al.*, 2003. Effects of natural and simulated herbivory on spine lengths of *Acacia drepanolobium* in Kenya. *Oikos*, 101: 171-179.