POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	57	3	573–579	2009

Short research contribution

Bingru LIU[1], Yanjiang LUO[2]

[1] Key Laboratory of Arid and Grassland Ecology at Lanzhou University,
Ministry of Education, Lanzhou 730000, China, e-mail: bingru.liu@163.com
[2] Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla,
Yunnan 666303, China, e-mail: yanjiang.luo@gmail.com (*corresponding author*)

RELATIONSHIP BETWEEN SEED SIZE AND PLANT ABUNDANCE IN AN ALPINE MEADOW OF THE QINGHAI-TIBETAN PLATEAU

ABSTRACT: Theoretical and field studies on seed size and plant abundance relationship have been conducted in various communities. However, inconsistent patterns have emerged from these studies, and still little is known about alpine meadows. Here we identified four models and their predictions: the seed size/number trade-off model (SSNTM), the succession model (SM), the spatial competition model (SCM), and the triangle model (TM), in order to assess the relationship between seed size and abundance in alpine meadows, and to elucidate underlying mechanisms. The study site was situated on the eastern Qinghai-Tibetan Plateau at 3500 m above sea level. From 1999 through 2001, two indices of plant abundance (aboveground biomass and density) were simultaneously measured in 45 quadrates (0.25 m^2). Data for 101 plant species (mostly Cyperaceae, Poaceae, Asteraceae, Ranunculaceae and forbs) showed that seed size is like log normal distributed, and it slightly skewed in smaller-sized seeds. The SSNTM, the TM, the SM and the SCM models were not supported in this alpine meadow, and the relationship between seed size and abundance was always positive (although in some samples, the relationship was not significant). The positive correlation between seed size and abundance observed for some grassland communities was also demonstrated in the alpine meadow. It suggests that seed size depends on the plant growth form, but the biomass-density relationship is inconsistent with previous studies. This suggests that the measure of abundance used in these studies is not the only reason for inconsistency of seed size.

KEY WORDS: abundance, alpine meadow, aboveground biomass, density, seed size, Qinghai-Tibetan Plateau

Seed size has been suggested to be one of the key traits determining community dynamics, diversity (Rees 1995, Rees *et al.* 2001, Coomes and Grubb 2003, Khurana *et al.* 2006) and functional characteristics of plant species (Weiher *et al.* 1999, Westoby *et al.* 2002). Many ecologists have long been fascinated with the relationship of seed size and plant species abundance (Rabinowitz 1978, Mitchley and Grubb 1986, Rees 1995, Eriksson and Jakobsson 1998, Guo *et al.* 2000, Bruum 2001, Leishman and Murray 2001, Guo 2003, Murray and Leishman 2003, Moles *et al.* 2004, Murray *et al.* 2005). Rabinowitz (1978) originally reported a positive correlation between seed mass and plant abundance in a tall grass prairie in the United States. However, inconsistent patterns have been reported for various plant communities, with different mechanisms proposed to explain the diverse relationships:

1. *The seed size/number trade-off model* (SSNTM). Small-seeded species produce more propagates than do large-seeded species (Shipley and Dion 1992, Greene and Johnson 1993, Leishman and Murray 2001). Rees (1995) and Guo *et al.* (2000) suggested that seed size/number trade-off may account for the observed patterns of seed size and abundance. Leishman and Murray (2001) formally showed that SSNTM predicts an overall negative correlation between seed mass and biomass within a community.

2. *The triangle model* (TM). The prediction of the TM as proposed by Guo *et al.* (2000) is that small-seeded species may be abundant or rare, but large-seeded species are always rare. Spatial patterns of distribution and abundance are constrained by seed size within triangular envelopes, *i.e.*, small-seeded species have a greater range of abundance and occupy a greater number of sites than large-seeded species. Temporal patterns of abundance and distribution are similarly correlated with seed size, *i.e.*, small-seeded species are generally more abundant and occur in more years than large-seeded species.

3. *The succession model* (SM). The SM predicts that the relationship of seed size and abundance depends on the time elapsed since the last disturbance. Leishman (2001) found some evidence for this model, although it was not significant. In the early stages of succession, species with small seeds appear first due to their ease of dispersal and production of large numbers of seeds. This creates a negative seed mass- abundance relationship. In the late stages of succession, however, large-seeded species, which are good competitors in shaded environments, dominate. The seed size-abundance relationship then becomes positive. In the intermediate stage, there is no significant relationship between seed size and abundance.

4. *The spatial competition model* (SCM). The SCM was proposed by Tilman (1994), who found that the spatial habitat allows a potentially unlimited number of species to coexist. In this model, spatial heterogeneity and disturbance are not required, but there is plant-by-plant replacement in a habitat in which all species are limited by, and compete for, a single resource. This model assumes that species make a trade-off between colonisation and competitive ability (Leishman and Murray 2001). Tilman (1994) stated that there is no need for the relationship between competitive ability and the equilibrial abundance of a species, and that the poorest competitor can have the highest equilibrial abundance. Thus no relationship would be expected between seed size and abundance within plant communities.

In summary, the SSNTM predicts a negative relationship between seed size and abundance (Rees 1995), the TM predicts a triangular correlation between seed size and abundance (Guo *et al.* 2000), the SM predicts a positive, negative or no correlation between seed size and abundance depending on the elapsed time since disturbance (Leishman and Murray 2001), and the SCM predicts no correlation between seed size and abundance (Tilman 1994, Leishman and Murray 2001).

In alpine areas, cold temperatures, short growing seasons and frost damage can limit pollination, pollen tube growth and seed maturation (Forbis 2003), all resulting in a reduction in seed output (Kudo 1991). Many alpine species are primarily clonal and are therefore expected to have low rates of seedling establishment in stressful environments, which are usually dominated by long-lived perennials (Billings and Mooney 1968). However, the mechanisms underlying the relationship between seed size and abundance in alpine meadows are not well understood.

Our aim was to assess the relationship between plant abundance and seed size in alpine meadows, and to elucidate possible underlying mechanisms. Plant abundance is critical for determining trends in the seed size to abundance relationship; thus, two indices of plant abundance were measured simultaneously: aboveground biomass and the density of individual plants.

The study site was selected in Nima of Maqu Country (35°58'N, 101°53'E, 3 500 m a.s.l.), a typical alpine meadow on the eastern edge of the Tibetan Plateau in Gansu Province, China. The average temperature there is 1.2°C from 1999 to 2001, and there is no apparent four seasons with only warm season from May to October and cool season from November to April. The average annual precipitation was 620 mm over the last 35 years, and 85% of that rainfall was concentrated within the growing season from May through September. This area has 2580 h of sunshine and more than 270 frost days per year. The native vegetation was typical of alpine meadows, being largely dominated by a few graminoids, such as clonal plant *Kobresia humilis* (C.A. Mey. ex Trautv) Bergiev, *Poa poophagor* (Bor), *Scirpus pumilus* (Vahl), *Roegneria nutans* (Keng), *Elymus nutans* (Griseb), *Festuca ovina* (Linn), *Stipa aliena* (Keng), *Kobresia capillifolia* (Decne.) C.B. Clarke, and *Agrostis hugoniana* (Rendle), and by all kinds of forbs, such as *Anemone rivularis* (Buch.-Ham). The average above ground biomass is ranged from 70 to 100 g m^{-2} (dry mass).

Forty-five quadrates (50 × 50 cm each) were randomly selected in the alpine meadow with at least 5 m between individual plots. Data were collected in 1999, and again during 2000 and 2001, in August when the biomass reached a maximum. Biomass, cover and density of each species were investigated in every quadrate. Together 101 plant species were differentiated and they are Cyperaceae, Poaceae, Asteraceae, Ranunculaceae and forbs. Plants within the quadrates were clipped at soil level, sorted according to species, oven-dried at 80°C for 24 h and weighed. In some cases, an "individual" may represent the whole genet, whereas in most perennial species it represents ramets, operationally defined as the plant tissue originating from one single position of roots. For tussock grasses, whole tussocks were considered as the individuals.

Seeds of each species were collected continuously when they became mature in 2000, 2001, 2002 and 2003. Seeds were kept indoors and air-dried, and 100 seeds from each species were randomly selected from the pooled sample for seed mass measurements.

The seed mass, density (number of individuals per quadrate) and biomass data for every species were analysed separately. All statistics were performed using SPSS13.00 for Windows (Chicago, USA). Spearman's correlation was used to test the correlations. Differences obtained at a level of P <0.05 were considered significant, and P <0.1 was considered marginally significant.

Frequency of seed mass classes plotted on a logarithmic scale produced an approximately normal distribution, but seed size was slightly skewed toward smaller-sized seeds (Fig. 1). The seed mass of 101 plant species spanned four orders of magnitude from 10^{-2} to 10^{2} mg.

Plant species in the alpine meadow primarily comprise perennial cushion and rosette

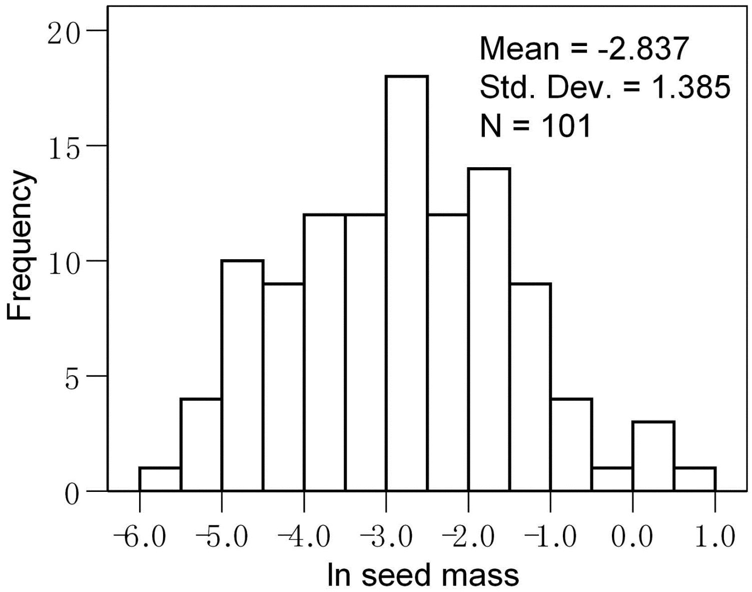

Fig. 1. Distribution of seed size of 101 plant species in plant communities at the study alpine meadow. Seed mass is given in g (dw) per 100 grains, and is log transformed.

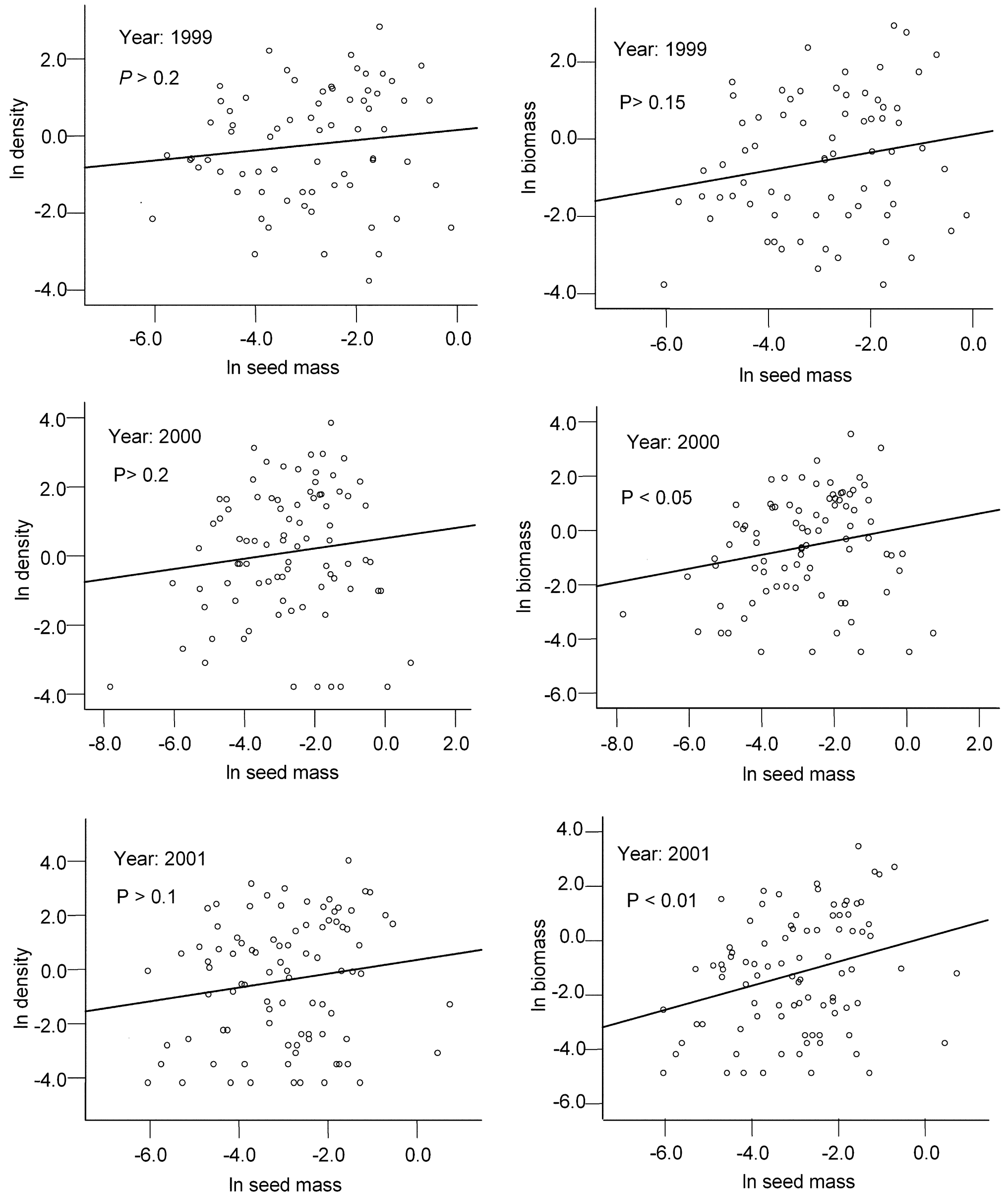

Fig. 2. The correlation between seed mass and density and above biomass in the alpine meadow for three years.

Note: all data are log transformed. Spearman's correlation coefficient (ρ) was used. All the relationships are positive. Statistically significant are only the relations in 2000 (*P* <0.05) and 2001 (*P* <0.01).

plants, forbs and graminoids with a maximum height of 20–40 cm. Few species are capable of completing their entire life cycle in a single year. Average aboveground biomass was 70–100 g m^{-2} (dry mass) with approximately 20–30 vascular plant species per quadrate (0.25 m^2). The predominance of specific plant groups was as follows: Cyperaceae + Poaceae> Asteraceae + Ranunculaceae> forbs.

The relationship between seed size and abundance was always positive, although in some samples it was not significant (Fig. 2). When using biomass as a measure of abundance, a significant positive correlation between seed size and biomass was found for the years 2000 (*P* <0.05) and 2001 (*P* <0.01). However, density values did not demonstrate a significant relationship with seed mass in any of the three years, although they all showed a positive trend.

Seed size in alpine meadow of eastern of the Qinghai-Tibetan Plateau showed an approximately normal distribution. The seed size of alpine plant species spanned four magnitudes from 10^{-2} to 10^{2} mg, which was consistent with a previous study conducted in this region (Bu *et al.* 2007), but slightly skewed toward smaller-sized seeds compared to larger-sized seeds in temperate and tropical zones, based on published values (Fenner and Thompson 2005). This may be due to lower net primary productivity (Zhang *et al.* 2004, Pluess *et al.* 2005), or the short growing season in a harsh environment, which constrains the upper level of seed mass by limiting the time available for seed maturation (Bondeau *et al.* 1999, Moles *et al.* 2007).

Among the many theories concerning seed size and abundance, the SSNTM makes some clear predictions regarding the relationship between seed size and abundance (Moles *et al.* 2004). The basis for the SSNTM is that seed size determines the competitive ability of seedlings, where large-seeded propagules always outcompete small-seeded ones. There is a trade-off between seed size and the number of seedlings within a species. Consequently, large-seeded species can invade within sites because of their competitive superiority, and small-seeded species can invade because they are more prolific and hence competitively superior with respect to dispersal between sites (Rees 1995, Eriksson and Jakobsson 1998, Eriksson 2005). In other words, the SSNTM predicts an overall negative correlation between seed mass and biomass within a community. This has been suggested as a potentially important mechanism for determining plant community composition.

In this study, seed mass was positively correlated with abundance as measured in terms of biomass, which is consistent with many experimental studies (Mitchley and Grubb 1986, Coomes *et al.* 2002, Levine and Rees 2002). Interestingly, when abundance was measured as the density of plant individuals, the relationship between seed mass and abundance was also positive, but only marginally significant. This is inconsistent with previous studies in which plant biomass or cover was negatively related to density (Chiarucci *et al.* 1999, Röttgermann *et al.* 2000, Guo 2003). The SSNTM was thus not supported in this alpine meadow.

The TM predicted that small-seeded species can be abundant or rare and broadly or narrowly distributed, but larger-seeded species are always rare and distributed in fewer sites. For annual plants in the desert, small-seeded species may be abundant or rare, but large-seeded species are always rare because small-seeded species produce more seeds, are more vagile, and persist longer in seed banks than do large-seeded species (Guo *et al.* 1999). This pattern may be due to a trade-off between seed size and number, increased dispersibility of small seeds and increased post-dispersal survival of small seeds and persistence in the seed bank (Guo *et al.* 2000). Many dominant alpine species found at our study site are long-lived perennials, and we found no evidence of a triangular correlation between seed size and abundance.

The predictions of the SM were dependent on the time elapsed since disturbance. The positive association observed between seed size and abundance in studies using cover as a measure of abundance is expected in crowded vegetation (competitive situations) in later stages of succession (Leishman and Murray 2001). This is because over time, smaller-seeded species are gradually replaced by larger-seeded species, and larger-seeded species come to dominate the existing vegetation. Our finding does not support the SCM, as this model predicts neither a positive nor negative relationship between seed size and abundance.

Our results suggested that there is positive correlation between seed mass and abundance, which is inconsistent with some previous studies *e.g.* Rabinowitz (1978) and Mitchley and Grubb (1986) found positive correlations between seed mass and abundance in tall grass prairie in the United States and chalk grassland communities in the United Kingdom, respectively, and the large-seeded species were tall and dominant while the small-seeded species occupied the interstices. Thus an alternative explanation for positive seed size and abundance correlations might be that both seed size and abundance are positively correlated with large growth forms, and abundant species tend to be those with larger growth forms Leishman *et al.*

(1995) also found consistent positive associations between growth form/plant height and seed mass among five temperate floras. Leishman and Murray (2001) suggested that both seed size and plant abundance may be positively correlated with growth forms. Thus the positive correlation between plant size and seed size may contribute to the explanation for the positive correlation found between abundance and seed size in some communities. In this study, the sequence of dominance of the plant groups was as follows: Cyperaceae + Poaceae> Asteraceae + Ranunculaceae> forbs. This suggested that abundant species tend to be those with larger growth forms, which tend to be more dominant, and that seed size in an alpine meadow may be depend on plant growth forms.

When patterns of seed size and abundance are interpreted in terms of the models, the measure of abundance should reflect the theoretical basis of the model. In the literature, abundance has generally been measured as either density or as cover (or biomass, which is positively related to cover, Chiarucci *et al.* 1999), thus plant biomass or cover should be negatively related to density (Guo 2003). However, in our study, the relationship between seed size and abundance was always positive with respect to both abundance indices measured as biomass and density, respectively. This suggests that the measure of abundance is not the only reason for inconsistency with respect to seed size. It is likely that the correlation between seed size and abundance in our alpine meadow was affected by alpine plant species interactions. Choler *et al.* (2001) and Callaway *et al.* (2002) revealed that both facilitative and competitive interactions are operating in alpine plant communities, and the interactions among plants are predominantly positive in alpine plant communities, whereas competition prevails in subalpine plant communities. Wang *et al.* (2008) suggested that inter-species facilitation (positive interactions) is possibly the dominant interaction within the alpine meadow plant community of the eastern Qinghai-Tibetan Plateau.

We believe that the correlation between seed size and abundance is not only affected by plant growth form, but also by other processes, such as facilitation (positive interactions between plants) in the alpine meadow. We also believe that the relationship between seed size and plant abundance may be the result of both long-term ecological selective pressures over time, and the constraints of the established evolutionary history of taxonomic affiliations in alpine meadows.

ACKNOWLEDGEMENTS: We thank many colleagues and students in Lanzhou University. We are grateful to Prof. Anna Hillbricht-Ilkowska and Janusz Uchmański from Centre for Ecological Research, Polish Academy of Sciences, for their excellent suggestions and corrections. We would also like to thank Prof. Cedar Bough Saeji for her help with the English.

REFERENCES

Billings W.D., Mooney H.A. 1968 – The ecology of arctic and alpine plants – Biol. Rev. 43: 481–529.

Bondeau A., Kicklighter D.W., Kaduk J. 1999 – Comparing global models of terrestrial net primary productivity (NPP): importance of vegetation structure on seasonal NPP estimates – Glob. Change Biology, 5: 35–45.

Bruum H.H. 2001 – On the seed mass-regional abundance relationship: the Eriksson & Jakonbsson (1998) model does not apply to Danish grasslands – J. Ecol. 89: 300–303.

Bu H., Ch X., Xu X., Du G. 2007 – Seed mass and germination in an alpine meadow on the Tsinghai-Tibet plateau – Plant Ecol. 191: 127–149.

Callaway R.M., Brooker R.W., Choler. P. 2002 – Positive interactions among alpine plants increase with stress – Nature, 417: 844–848.

Chiarucci A., Wilson J.B., Anderson B.J., De Mominicis V. 1999 – Cover versus biomass as an estimate of species abundances: does it make a difference to the conclusions? – J. Veg. Sci. 10: 35–42.

Choler P., Michalet R., Callaway R.M. 2001 – Facilitation and competition on gradients in alpine plant communities – Ecology, 82: 3295–3308.

Coomes D.A., Grubb P.J. 2003 – Colonization, tolerance, competition and seed-size variation within functional groups – Trends Ecol. Evol. 18: 283–291.

Coomes D.A., Rees M., Grubb P.J. 2002 – Are differences in seed mass among species important in structuring plant communities? Evidence from analyses of spatial and temporal variation in dune-annual populations – Oikos, 96: 421–432.

Eriksson O., Jakobsson A. 1998 – Abundance, distribution and life histories of grassland plants: a comparative study of 81 species – J. Ecol. 86: 922–933.

Eriksson O. 2005 – Game theory provides no explanation for seed size variation in grasslands – Oecologia, 144: 98–105.

Fenner M., Thompson K. 2005 – The ecology of seeds – Cambridge University Press, London, pp. 47–97.

Forbis T.A. 2003 – Seedling demography in an alpine ecosystem – Am. J. Bot. 90: 1197–1206.

Greene D.F., Johnson E.A. 1993 – Seed mass and dispersal capacity in wind-dispersed diasporas – Oikos, 67: 69–74.

Guo Q., Rundel P.W., Goodall D.W. 1999 – Structure of desert seed banks: comparisons across four North American desert sites – J. Arid Environ. 42: 1–14.

Guo Q., Brown J.H., Valone T.J. 2000 – Constraints of seed size on plant distribution and abundance – Ecology, 81: 2149–2155.

Guo Q. 2003 – Plant abundance: the measurement and relationship with seed size – Oikos, 101: 639–642.

Khurana E., Sagar R., Singh J.S. 2006 – Seed size: a key trait determining species disturibution and diversity of dry tropical forest in northern India – Acta Oecol. 29: 195–204.

Kudo G. 1991 – Relationships between Flowering Time and Fruit Set of the Entomophilous Alpine Shrub, *Rhododendron aureum* (Ericaceae), Inhabiting Snow Patches – Am. J. Bot. 80: 1300–1304.

Leishman M.R., Westoby M., Jurado E. 1995 – Correlates of seed size variation: a comparison among five temperate floras – J. Ecol. 83: 517–530.

Leishman M.R. 2001 – Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality – Oikos, 93: 294–302.

Leishman M., Murray B.R. 2001 – The relationship between seed size and abundance in plant communities: model predictions and observed patterns – Oikos, 92: 151–161.

Levine J.M., Rees M. 2002 – Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization – Am. Nat. 160: 452–467.

Mitchley J., Grubb P.J. 1986 – Control of relative abundance of perennials in chalk grassland in southern England – J. Ecol. 74: 1139–1166.

Moles A.T., Ackerly D.D., Tweddle J.C. 2007 – Global patterns in seed size – Global Ecol. Biogeogr. 16: 109–116.

Moles A.T., Falster D.S., Leishman M.R. 2004 – Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime – J. Ecol. 92: 384–396.

Murray B.R., Kelaher B.P., Hose G.C. 2005 – A meta-analysis of the interspecific relationship between seed size and plant abundance within local communities – Oikos, 110: 191–197.

Murray B.R. Leishman M. 2003 – On the relationship between seed mass and species abundance in plant communities – Oikos, 101: 643–645.

Pluess A.R., Schütz W., Stöcklin J. 2005 – Seed weight increase with altitude in Swiss Alps between related species but not among populations of individual species – Oecologia, 144: 55–61.

Rabinowitz D. 1978 – Abundance and diaspore weight in rare and common prairie grasses – Oecologia, 37: 213–219.

Rees M., Condit R., Crawley M., Pacala S., Tilman D. 2001 – Long-term studies of vegetation dynamics – Science, 293: 650–655.

Rees M. 1995 – Community structure in sand dune annuals: is seed weight a key quantity? – J. Ecol. 83: 857–886.

Röttgermann M., Steinlein T., Beyschlag W. 2000 – Linear relationships between aboveground biomass and plant cover in low open herbaceous vegetation – J. Veg. Sci. 11: 145–148.

Shipley B., Dion J. 1992 – The allometry of seed production in herbaceous angiosperms – Am. Nat. 139: 467–483.

Tilman D. 1994 – Competition and biodiversity in spatially structured habitats – Ecology, 75: 2–16.

Wang Y., Chu C., Maestre F.T., Wang G. 2008 – On the relevance of facilitation in alpine meadow communities: An experimental assessment with multiple species differing in their ecological optimum – Acta Oecol. 33:108–113.

Weiher E., van der Werf A., Thompson K. 1999 – Challenging Theophrastus: a common core list of plant traits for functional ecology – J. Veg. Sci. 10: 609–620.

Westoby M., Falster D.S., Moles A.T. 2002 – Plant ecological strategies: some leading dimensions of variation between species – Annu. Rev. Ecol. Syst. 33: 125–59.

Zhang S.T., Du G.Z., Chen J.K. 2004 – Seed mass in relation to phylogeny, growth form and longevity in a subalpine meadow on the east of the Tibetan Plateau – Folia Geobotanica, 39: 129–142.

Received after revision September 2008