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Original Article

# Influence of Underground Storage on Seed Weight of Perennial Plants in Mongolia

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## Abstract

**Key words**: photosynthetic productivity, underground storage, seed weight

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There are a number of studies on relevance of photosynthetic contribution for seed weight. Here we demonstrate a contribution of plant underground storage on seed weight. We collected 348 seed samples of 230 species, in the forest-steppe, steppe, desert-steppe and desert zones in Mongolia, between 1981 and 2007. All species were categorized by growth form, flowering phenology and underground storage. Plant height was not different among categories of flowering phenology and underground storage. Seed weight was higher in large storage perennials than in small storage species. Correlation between seed weight and plant height was significantly positive in small storage perennials but it was insignificant in large storage perennials. For small storage perennials, correlation between seed weight and plant height was found in early and continuous flowering perennials while was absent in late flowering perennials. For large storage perennials, seed weight and plant height positively correlated in early flowering perennials, but those were not correlated and negatively correlated in continuous and late flowering perennials, respectively. The results suggest that early and continuous flowering perennials might use photosynthetic production for seed development, more intensive than late flowering perennials. Also, late flowering perennials more strongly use underground storage for seed development.

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## Introduction

Seed weight at least partly reflects phylogenetic signals (Thompson, 1990; Grime *et al*., 1997; Knight & Ackerly, 2002). Most studies agree that seed weight is associated to plant traits, such as growth form (Eriksson, 2016; Ackerly, 2009; Albach & Greilhuber, 2004), phenology (Zhang, 1998) and photosynthetic productivity (Liu *et al*., 2012; Knight *et al*., 2005). Annual plants produce smaller seeds than perennials (Sera & Sery, 2004), and herbs generally make smaller seeds than shrubs (Moles *et al.,* 2005). Leishman *et al.* (1995) reported that mean log seed weight of climbers is large, followed by woody plants, then forbs and graminoids, thus pointing to seed weight differences among growth forms. Among annual and perennial plants, onset of flowering is positively and – respectively - negatively correlated with seed mass (Zhang, 1998; Bolmgren & Cowan, 2008). Seed size and seed mass are strongly associated to plant height (Leishman *et al*., 1995; Moles *et al*., 2004). Experimental results showed e.g. that seed weight is greatest for pruned *Ambrosia trifida* individuals with intact root systems (Bazzaz & Carlson, 1979), and seed weight and leaf area are positively correlated in soybean (Park *et al*., 2013), indicating photosynthetic effect on seed weight in annuals.

A $^{13}C$ tracing experiment revealed that young fruits are photosynthetically active, while photosynthetic products from leaves were mainly transferred to the below-ground parts

(Horibata *et al*., 2007). Translocation to fruits was very small even when fruit photosynthesis was restricted by the artificial shading. Amartuvshin and Ochgerel (2016) suggested that underground-storage in perennials might be important for seed development. Hence, we hypothesized that photosynthetic production contributes directly to seed development of annuals and shrubs. In addition to photosynthetic production, underground storage might support seed development in perennials. The purpose of this study is to describe (1) whether underground storage is contributed to seed weight of perennials, and (2) to explain mechanisms.

## Material and Methods

The climate of Mongolia is continental, with cold-dry winters and warm-wet summers. Precipitation gradually decreases and air temperature increases, as well as climatic aridity increases from the forest-steppe to desert in Mongolia (Pyankov *et al*., 2000).

We collected 348 seed samples of 230 species in the forest-steppe, steppe, desert-steppe and desert zones in Mongolia (Fig. 1), between 1981 and 2007. For analyses, we used 72, 224 and 52 of samples in annual/biennials, perennials and shrub/tree species; representing 190, 100 and 58 of seed samples in early, late and continuous flowering species, and 74, 139 and 135 in species with no-, small and large underground storages, respectively.

When plants shed seeds, we harvested fruits with seeds and then dried those in paper bags at room temperature. The seeds were randomly sampled at each site. Seed maturity in each site was evaluated by maximum weight of dry seeds as reported by Harrington (1972). Weight of a hundred seeds was measured 10 times in each seed sample, using the analytic scale Shimadzu AY220 (d-0.1 mg). Coefficient of variation of seed weight within seed sample was less than 3.0%, indicating seed weight was correctly measured. Plant height has a direct positive effect on production (Gustafsson & Norkko, 2019). Then, we used plant height as a proxy for primary production and collected plant height data according to Grubov (1982), Jigjidsuren and Johnson (2003). Growth form was divided into three categories as annual/biennial, perennial and shrub/tree. The latter were divided according to plant height: shrubs into two groups, such as short (<100 cm) and tall (>100 cm). Flowering phenology was classified into three categories viz. early flowering (earlier than July), late flowering (later than July) and continuous flowering (from May to September).

Kaul (1985) and Hendry (1987) classified organs of underground storage in plants. We used three categories, such as no-storage (annuals/biennial), small storage (fibrous root and taproot without nitrogen fixation) and large storage (bulb, stolon, rhizome, tuberous taproot and taproot with nitrogen fixation).


Figure 1. Localities of seeds sampled across Mongolia.

Based on seed samples, we calculated mean seed weight (MSW) and standard error (SE) per species. Overall mean seed weights and standard error were calculated for each category of growth form, flowering phenology and underground storage, and compared among categories. To detect contribution of photosynthetic production for seed development, we calculated correlation between seed weight and plant height within each of the mentioned categories. Photosynthetic production was regarded important for seed development, if correlation between seed weight and plant height was significantly positive, and photosynthetic production was important for seed development more than underground storage, if it was insignificant. Underground storage was important for seed development nearly equal and/or more than photosynthetic production, if correlation between seed weight and plant height was significantly negative.

To compare seed weight among categories of growth form, flowering phenology and underground storage, we used one-way ANOVA and Tukey HSD test, based on $\log_{10}$ transformed data on seed weight and plant height for analysis. Also, to calculate correlations of seed weight and plant heights in each category of growth form, flowering phenology and underground storage, we used Pearson's Correlation Coefficient. Statistics were done in the software IBM SPSS 24.

## Results

Plant height was indifferent among all categories, except for the difference between height of shrubs/trees towards all others. Also, plant height was not different among categories of flowering phenology and underground storage (Table 1), suggesting not all small plants have large underground storage. A hundred seed weights were significantly different among categories of growth form (ANOVA, $p<0.05$), flowering phenology (ANOVA, $p<0.05$, Fig. 2a) and amount of underground storage (ANOVA, $p<0.05$, Fig. 2b). Seeds were heavier in tall shrubs than in short (ANOVA, $p<0.05$). Seed weight was lighter in annual/biennials than in perennials and shrub/trees (Table 1). Early flowering plants produced heavier seeds than late and continuously flowering plants. Large storage plants produced heavier seeds than no-storage and small storage ones (Fig. 2b).

In our dataset, seed weight was correlated positively with plant height (Fig. 3a), in annuals/biennials ($r=0.31$, $p=0.009$), perennials ($r=0.22$, $p=0.001$) and shrubs/trees ($r=0.46$, $p=0.002$). Thus correlations were weaker in perennials than in annual/biennials and shrub/trees. Correlation of seed weight and height was positive within early ($r=0.34$, $p<0.0001$) and continuous flowering plants ($r=0.65$, $p<0.0001$), while it was insignificant in late flowering plants ($r=-0.02$, $p=0.88$). Moreover, correlations of those variables were significantly positive within no- (Fig. 3b) and small storage plants (Fig. 3c) while they were insignificant in large storage plants (Fig. 3d).

The correlation between seed weight and plant height was significantly positive within small storage perennials ($r=0.27$, $p=0.009$) but it was insignificant in large storage ones ($r=0.1$, $p=0.25$). For flowering phenology, the correlation was significantly positive in early flowering

Table 1. Comparison of plant height among categories of growth forms, flowering phenology and underground storage.

| | Category | Plant height* (cm) |
|---|---|---|
| Growth form | Annual/biennials | 53.4±1.6b |
| | Perennials | 49.0±1.2b |
| | Shrubs/trees | 100.9±5.7a |
| Flowering phenology | Early flowering | 53.4±1.6b |
| | Continuous flowering | 58.6±2.4b |
| | Late flowering | 57.1±1.8b |
| Underground storage | No storage | 53.9±1.6b |
| | Small storage | 56.0±1.9b |
| | Large storage | 68.3±4.1b |

*Different letters indicate significant differences of Tukey HSD test ($p<0.05$).

annuals ($r$=0.47, $p$=0.02) but insignificant in continuous flowering ($r$=0.46, $p$=0.08) and late flowering annuals ($r$=0.35, $p$=0.06). Similarly, it was significantly positive in early ($r$=0.35, $p$<0.0001) and continuous flowering perennials ($r$=0.61, $p$<0.0001), whereas there was no correlation in late flowering perennials ($r$=-0.18, $p$=0.18). For shrubs/trees, we used two categories for correlation analysis, because we had a limited number of seed samples for each group. Correlation between seed weight and height was significantly positive within both early ($r$=0.41,

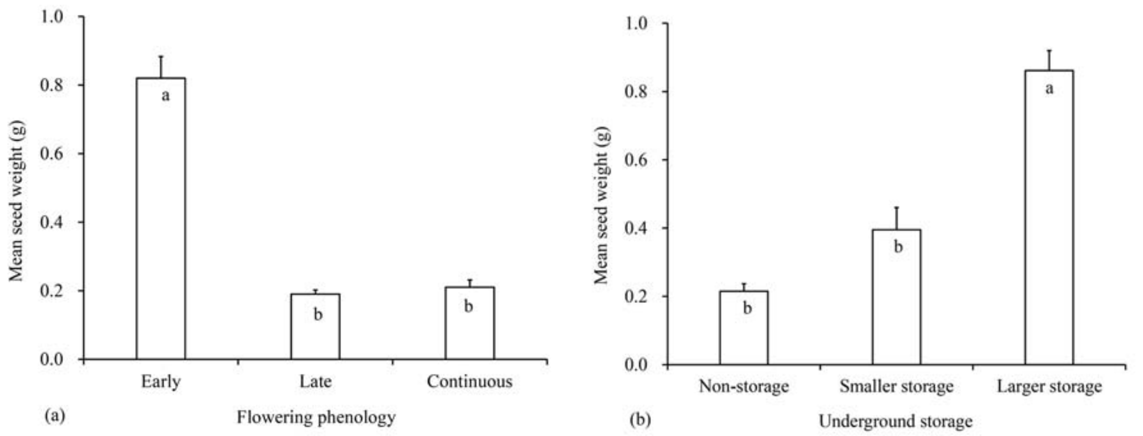


Figure 2. Correspondence of mean seed weight with (a) flowering phenology (Tukey HSD test, $p$<0.05) and (b) amount of underground storage (Tukey HSD test, $p$<0.05). Bars indicate Mean±SE.

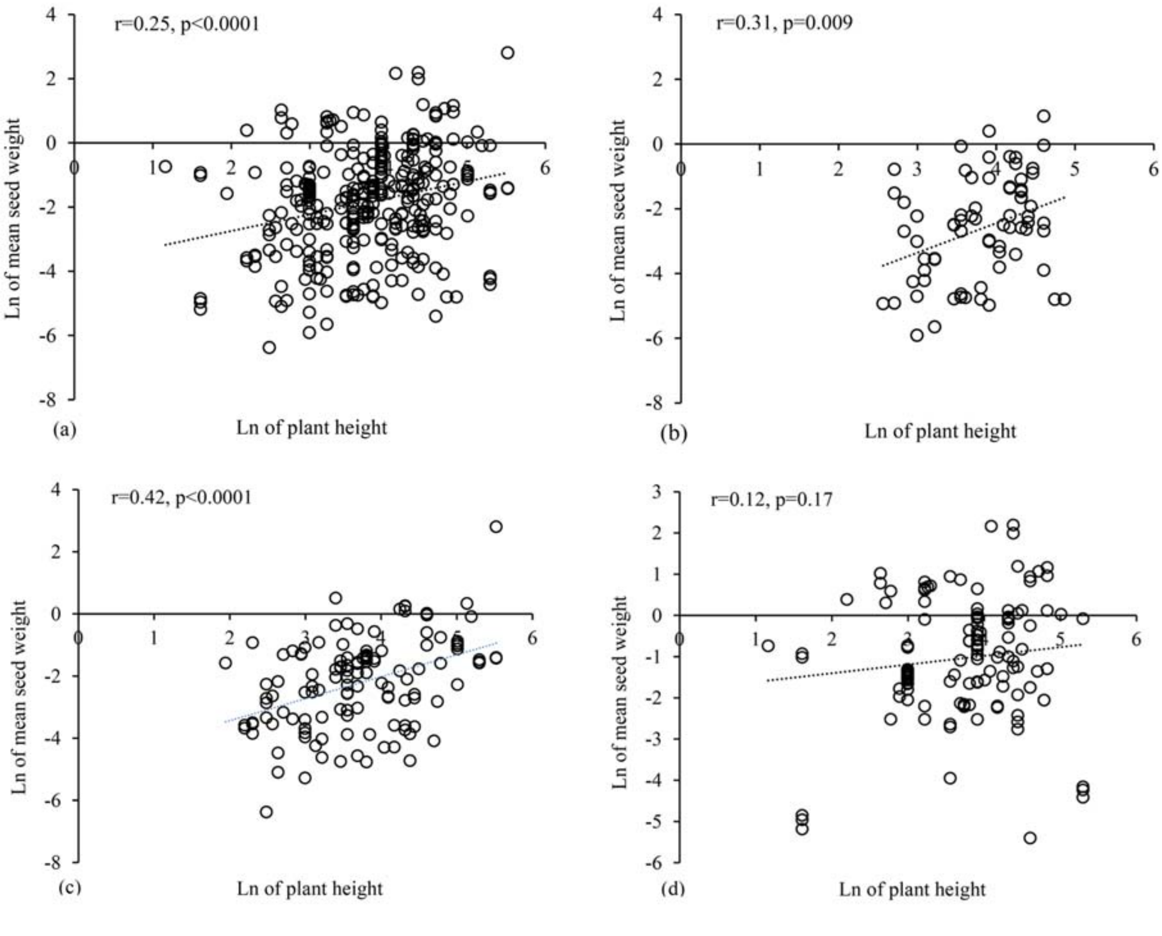


Figure 3. Correlations between mean seed weight and (a) height of all plants, (b) of no storage, (c) small storage and (d) large storage plants.

Table 2. Correlation coefficients between seed weight and plant height in categories of flowering phenology and underground storage.

| Underground storage | Flowering phenology | | |
|---|---|---|---|
| | Early | Continuous | Late |
| No storage | 0.47* | 0.46 | 0.35 |
| Small storage | 0.41** | 0.75** | 0.001 |
| Large storage | 0.38** | 0.48 | -0.35* |

* – $p<0.05$, ** – $p<0.01$

*p*=0.04) and continuous/late flowering shrub/trees (*r*=0.51, *p*=0.03). Within early flowering plants, correlation between seed weight and height was positive within all categories of underground storage. Within continuous flowering plants, the correlation was positive within no- and small storage plants, but insignificant in large storage one. Within late flowering plants, it was insignificantly positive in no- and small storage plants, while significantly negative in large storage plants. In early and continuous flowering plants, all categories of underground storage keep significant positive correlation between seed weight and height, excluding insignificance for large storage and continuous flowering plants. In late flowering plants, no- and small storage plants showed insignificant correlations between those variables while large storage plants showed significant negative correlation (Table 2).

## Discussion

Earlier studies have reported that seed weight differs among growth forms (Leishman *et al*., 1995; Sera & Sery, 2004; Moles *et al*., 2005), and between annuals (Boerma & Ashley, 1987; Singal *et al*., 1995; Egli & Bruening, 2004; Weber *et al*., 2005), perennials (Yu *et al*., 2013) and shrubs (Yoshimichi & Hiromi, 1993). Our results support the hypothesis that seed weight is lower in annuals than in other growth forms. Also, tall shrubs produced heavier seeds, compared with short shrubs. Previous and our results indicate that photosynthetic production is useful for seed development of annuals and shrubs. However, seed weight was lighter in small storage perennials than in large storage ones, suggesting perennials might use both photosynthetic production and underground storage for seed development. Also, heavier weighted seeds of early flowering and large storage plants suggest that ephemeral perennials might use underground storage for seed development.

Researchers found positive correlations of seed size/weight with plant height in flowering plants (Moles *et al*., 2004, 2005; Thomson *et al*., 2011), with leaf length and width in annuals (Chung *et al*., 1998), and with height in shrub/trees (Jardim & Batalha, 2008). Our results on correlation between seed weight and height confirm results of the previous studies. We also found this correlation in no-, and small storage categories, because of influence of a photosynthetic production for seed development. Correlation between seed weight and height was significantly positive in early and continuous flowering plants, indicating that those plants use photosynthetic production for seed development. The lack of correlation between seed weight and height in late flowering plants suggest that late flowering plants also use underground storage for seed development, because plant height was not different among categories of flowering phenology.

Hori and Tsuge (1993) reported that maximum net photosynthesis of leaves and bracts on *Carpinus laxiflora* tree is essentially constant from May to early August but subsequently decreased gradually, while seed weight increased rapidly during early development, from middle May to early July. Also, Yu *et al.* (2013) reported that photosynthetic production from sepals in the perennial *Paris polyphylla* is involved in fruit growth and seed development, and that developing fruit and rhizomes compete for photosynthetic production exported by leaves.

Positive correlation between seed weight and plant height in annual/biennials was kept during flowering phenology, indicating that annual/biennials use photosynthetic production for seed development during summer season. Significance and insignificance of the correlations show decreasing photosynthetic activity of annual/

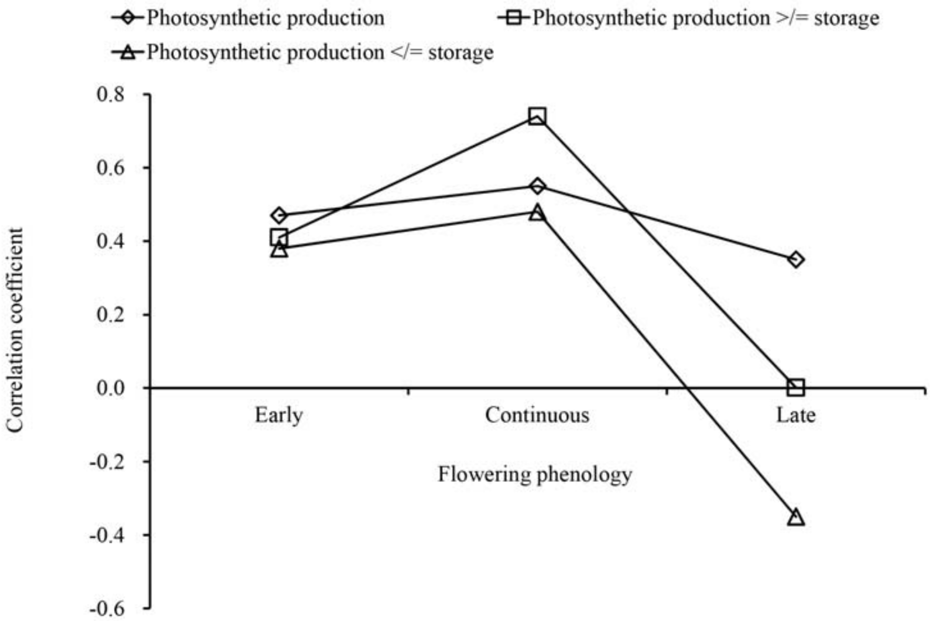


Figure 4. Correlation coefficient between seed weight and plant height in categories of flowering phenology and mechanism for seed development.

biennials from early to late flowering phenology.

In small storage perennials, the correlation between seed weight and height was significant in early and continuously flowering species, whereas it was insignificant in late flowering category.

The correlations indicate that photosynthetic production might be useful for small storage perennials in early and continuous flowering phenology but less useful in late flowering phenology. In large storage perennials, the correlations were significantly positive in early flowering category but insignificant and significant negative in continuous and late flowering categories, respectively. It means that photosynthetic production is also contributing to large storage perennials in early flowering phenology, more so than for those with later phenology. Even so, productivity directly contributes in those with continuous flowering phenology, more than in late flowering one (Fig. 4). Our results suggest that large storage perennials might use underground storage for seed development if they display late flowering phenology.

Leaves of no-storage and small storage plants grow on the stems but those of large storage plants mostly start to grow from rhizomes or bulbs (Jigjidsuren & Johnson, 2003). Previous studies as well as our results suggest that photosynthetic production in no-storage and small storage plants directly move from leaves to seeds through stems, while in large storage plants, it is transferred to rhizomes and bulbs. For large storage plants, underground storage might be firstly used for seed development, and photosynthetic production is employed to fill underground organs, respectively.

The results of this study suggest that early and continuous flowering perennials use photosynthetic production for seed development, more intensive than late flowering perennials. Also, late flowering perennials more intensively build on underground storage for seed development.

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