

Original Article

Normalized Seed Weight of Three Species of the Genus *Peganum* L. (Peganaceae Van Tieghem) in Mongolia

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Abstract

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Variation of seed weight of *Peganum* species is positively correlated with mean seed weight in big populations. It was insignificant in small populations, suggesting normalized seed weight is useful to distinguish the population sizes. Normalized seed weight is increased with increasing aridity index and precipitation amount in most sites. Within populations of *Peganum harmala*, variation of seed weight and normalized seed weight corresponded to Nei's diversity index, while within other species, mean seed weight corresponded to Nei's diversity index. The normalized seed weight was lowest in human-dispersal species, highest in hydro-dispersal species, but it was moderate in wind-human-dispersal species. Low normalized seed weight is associated to species with low genetic diversity, while high normalized seed weight to species with high genetic diversity. Variation of seed weight was related with precipitation and climatic aridity and genetic diversity within species and mean seed weight was with climatic aridity and genetic diversity within species, but normalized seed weight was related with precipitation, climatic aridity and genetic diversity inter- and within species.

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Introduction

Evolution of seed weight is governed by climatic (Zhang, 1998; Moles *et al.*, 2005; Liu *et al.*, 2014) and genetic factors (Ohto *et al.*, 2005; Cai *et al.*, 2012). The climatic factors, such as temperature and precipitation had much less explanatory power than did plant traits, such as seed dispersal syndrome (Tiffney, 2004) and plant growth form (Eriksson, 2000).

Variations of seed weight between or within plant species are due to the evolutionary responses of plants (Zhang, 1998; Doganlar *et al.*, 2000). Meyer (1997) reported that seed weight (named as *seed mass*) is increased with a decreasing climatic aridity, while Harel *et al.* (2011) found that seed weight decreased with increasing aridity and rainfall variability. Seed

weight positively correlated with precipitation, and temperature (Busso & Perryman, 2005; Moles *et al.*, 2005). Stromberg & Boudell (2013) concluded that small seed weight is independently associated with wet and disturbed conditions in dryland riparian ecosystems.

Genetic diversity is useful in understanding the evolutionary relationships of different taxa (Kresovich & McFerson, 1992; Booy *et al.*, 2000; Ohto *et al.*, 2005). The larger populations with low levels of disruption have the highest genetic diversity (Maguire & Sedgley, 1997). Lammy *et al.* (1999) suggested that genetic diversity is usually low in isolated populations as a consequence of genetic drift, inbreeding, bottlenecks and founder effects. Quantitative

genetic analyses showed that seed weight has a relatively high heritability (Fatokun *et al.*, 1992; Giroux *et al.*, 1996; Doganlar *et al.*, 2000; Cai *et al.*, 2012). Teng *et al.* (2009) suggested that the QTL and environmental interaction (QE) effects might significantly alter seed weight during seed development.

Populations that had larger mean seed weights also had larger maximum and minimum seed weights (Zhang, 1998), suggesting weight variation increases with increasing mean seed weight. Narantsetseg (2012) suggested that more than two cotyledons might be related with genetic drift. Hence, mean seed weight may increase by polyploidy and variation of seed weight increase by genetic drift, bottlenecks and founder effects.

Iljin (1958) suggested that evolutionary, *P. harmala* is older than *P. multisectum* and *P. nigellastrum*. Diversity in DNA sequences among *Peganum* species was found (Zhao *et al.*, 2011). Seeds of *P. harmala* and *P. multisectum* disperse by only human activities and water flow, while those of *P. nigellastrum* by both wind and human activities. Growth form of *P. harmala* and *P. multisectum* is main root, but that of *P. nigellastrum* is stolon (Amartuvshin *et al.*, 2006).

We hypothesized that in genus *Peganum* L., normalized seed weight might contribute with climatic and genetic factors and indicate evolutionary response of species, better than mean seed weight and variation of seed weight. The purpose of this study was to describe (1) whether mean seed weight, variation of seed weight or normalized seed weight within *Peganum* L. genus is contributed with climatic and genetic variability and (2) what seed weight variability is contributed to evolution.

Materials and Methods

Climatic data is given based on database of Institute of Meteorology and Hydrology of Mongolia, and the data of nearest weather stations with seed sampling sites were used (Table 1). Based on long-term averaged air temperature and averaged sum precipitation, de Martonne aridity index (Oliver & Fairbridge, 1987) was calculated using the formula $AI = P / (T+10)$, where P is long-term averaged sum precipitation and T is long-term averaged air temperature. The minimum absolute value of aridity index correspond to the maximum climatic aridity.

Table 1. Climatic data in each seed collected site of three *Peganum* species in Mongolia.

Species name	Year of seed collection	Growth form	Seed dispersal	Aridity index	Precipitation (mm)	Air temperature (°C)
<i>P. harmala</i> L.	1983	Main root	Human	11.64	112.32	-0.35
	1983	Main root	Human	6.18	75.21	2.17
	1987	Main root	Human	7.01	98.33	4.03
	1992	Main root	Human	6.18	75.21	2.17
	1995	Main root	Human	5.18	89.64	7.30
	2001	Main root	Human	3.79	56.93	5.04
	<i>P. multisectum</i> (Maxim.) Bobr.	2000	Main root	Water flow	7.68	117.20
2000		Main root	Water flow	5.26	74.81	4.22
2000		Main root	Water flow	5.26	74.81	4.22
<i>P. nigellastrum</i> Bge.	1998	Stolon	Wind and human	8.88	122.61	3.81
	1998	Stolon	Wind and human	5.50	77.38	4.08
	1998	Stolon	Wind and human	8.88	122.61	3.81
	1999	Stolon	Wind and human	8.02	111.14	3.85
	2000	Stolon	Wind and human	7.68	117.20	5.27
	2000	Stolon	Wind and human	8.87	134.75	5.20
	2000	Stolon	Wind and human	8.87	134.75	5.20
	2000	Stolon	Wind and human	9.42	132.08	4.02
	2000	Stolon	Wind and human	5.26	74.81	4.22

Seed dispersal and growth form of the studied species were detected according to Amartuvshin *et al.* (2006). Seed samples of *P. harmala* were taken from the Mongolian Altai (in center of Mankhan district); Trans-Altai Gobi (in Ekhiin gol oasis); two sites in the Dzungarian Gobi (in Uench river basins and near Shiiriin us spring); two sites in Eastern Gobi (near well of herder camp between the districts Tsogt-Ovoo and Khankhongor, and in center of Khanbogd district, Umnugobi province).

The seed samples of *P. multisectum* were collected from three sites in the Gobi-Altai (in center of Sevrei district, in Baruun gol and near Bayasakh village). Those of *P. nigellastrum* were taken from one site in the Eastern Mongolia (Ongon sand dune) and one site in the Alashan Gobi (Noyon district) and two sites in the Valley of Lakes (near Orog lake) and 5 sites in the Gobi-Altai (Bayanlig and Bayandalai districts, the sand dune Khongor, Bayanzag and Moltso) (Fig. 1).

The seed collection at the Institute of Botany was used for observation of seedling morphology. In total, 18 seed samples were examined (Fig. 1), which was collected between

1983 and 2001, from above-mentioned regions. When plants shed seeds, we harvested capsules and then dried them in paper bags at room temperature. The seeds were sampled randomly in each site.

Seed maturity in each site was evaluated by weight of dry seeds as reported by Harrington (1972). Weight of a thousand seeds was measured in 10 times, using the analytic scale Shimadzu AY220 (d-0.1 mg). The C.V. of seed weight within seed sample was less than 3.0%, indicating seed weight was correctly measured. Hence, to calculate weight variation in each seed sample, we used discrimination between maximum and minimum weights and to calculate normalized seed weight, mean seed weight was divided into weight variation.

Seed germination was determined at $25\pm 1^{\circ}\text{C}$ for 10 days in the seed germinator, without dormancy breaking treatments, using Petri dishes and moist blotter by distilled water. Frequency of four, three cotyledons and different-shape dicotyledons counted on 1000 embryos in each seed sample. Based on their frequencies, we calculated Nei's genetic diversity index, using the formula $H = 1 - \sum p_i^2$, where p_i is

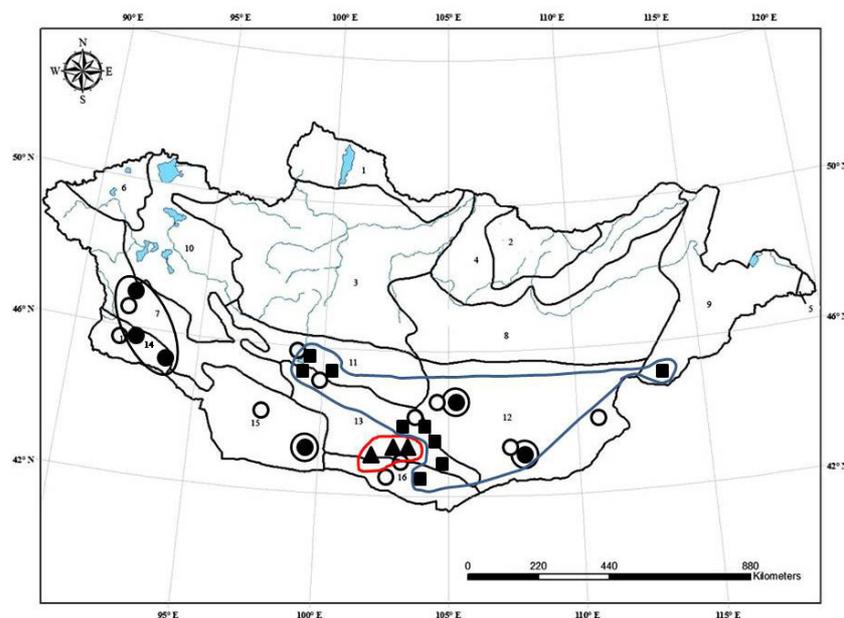


Figure 1. Seed sampled sites of *Peganum* species in Mongolia. Open circle – weather station, Solid circle – seed samples of *P. harmala*, Solid triangle – seed samples of *P. multisectum*, Solid square – seed samples of *P. nigellastrum*; Black line – sites of *P. harmala*; Red line – sites of *P. multisectum*; Blue line – sites of *P. nigellastrum*. Numbers indicate botany-geographic regions according to Grubov (2001): 1 – Khubsugul, 2 – Khentii, 3 – Khangai, 4 – Mongol Dauria, 5 – Khovd, 6 – Mongolian Altai, 7 – Great Khyangan, 8 – Middle Khalkh, 9 – Eastern Mongolia, 10 – Great Lake Depression, 11 – Valley of Lakes, 12 – Gobi-Altai, 13 – Eastern Gobi, 14 – Alashan Gobi, 15 – Trans-Altai Gobi, 16 – Dzungarian Gobi.

each frequency of more than two cotyledons (four and three cotyledons) and different-shape dicotyledons and normal dicotyledons; Σ represents the summation over all frequencies (Nei, 1973).

Population sizes (N) were corresponding approximately to the red-list categories of “critically endangered” and “endangered”, “vulnerable” respectively (Brook *et al.*, 2002). However, *P. harmala* widely distributes from Mediterranean to North America and Central Asia, and its main distribution range is in the Dzungaria, Mts. Tien Shan (Central Asia), but this species is categorized as very rare (Erdenejav, 1997) or vulnerable (Nyambayar *et al.*, 2011) in Mongolia. *P. multisectum* was registered in the Gobi-Altai, Mongolian province (Amartuvshin *et al.*, 2006), including north-western China (Zhao *et al.*, 2011). *P. nigellastrum* commonly distributes in the Mongolian province, Central Asia, including northern China (Zhao *et al.*, 2011) and Mongolia (Amartuvshin *et al.*, 2006). Hence, population sizes of *P. nigellastrum*, *P. multisectum* and *P. harmala* were evaluated as big or small. Within species, big population evaluated as distribution limited in valleys and river basins, and small population size as distribution limited in oasis, spring and around well.

One-way ANOVA was used to calculate correspondence between seed weight variability (variation of seed weight, mean seed weight and normalized seed weight), climatic variability (aridity, precipitation and air temperature) and genetic diversity (Nei’s genetic diversity). Tukey’s Post Hoc test was used to compare seed weight variability among species. Spearman Rank Correlation was used to calculate correlation between variation of seed weight with mean seed weight and variation of seed weight with aridity index and precipitation amount. Nomenclature follows that by Amartuvshin *et al.* (2006).

Results

Variation of seed weight is positively correlated with mean seed weight in big populations, but it was insignificant in small populations, suggesting normalized seed weight is useful to distinguish population sizes (Fig. 2).

Variation of seed weight and mean seed weight were not different among species,

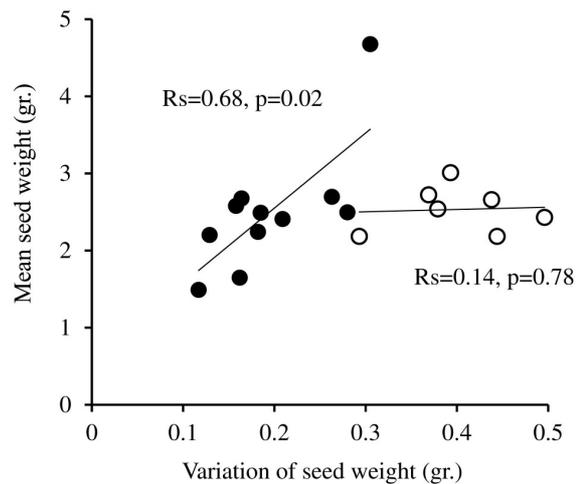


Figure 2. Correlation between variation of seed weight and mean seed weight in different population sizes. Solid circle – big populations, Open circle – small populations.

growth forms, seed dispersal types (Fig. 3A). Normalized seed weight was significantly different between *P. harmala* and *P. multisectum*, but that of *P. nigellastrum* was higher and lower than those of *P. harmala* and *P. multisectum*, respectively (Fig. 3B), indicating normalized seed weight is related with seed dispersal syndrome. However, *P. harmala* and *P. multisectum* have main root, whereas *P. nigellastrum* has stolon, and normalized seed weight of main root species was lowest or highest, but that of the stolon species was moderate. Population size of *P. harmala* is smaller than two other species, *P. multisectum* and *P. nigellastrum* with big population sizes. Normalized seed weight of species with small population size was low, but that of species with big population size was high.

More than two cotyledons were found in 0.0-11.0% of *P. harmala* and 0.0-2.0% of *P. multisectum* and *P. nigellastrum*. Different-shape dicotyledons were in 0.0-29.0% of *P. harmala*, but 0.0% in other two species. Both more than two cotyledons and different-shape dicotyledons showed higher frequencies in *P. harmala*, compared with two other species (Fig. 3C). The frequency of more than two cotyledons and different-shape dicotyledons was highest in human-dispersal species. Nei’s diversity index showed same pattern with frequency of more than two cotyledons and different-shape dicotyledons (Fig. 3D).

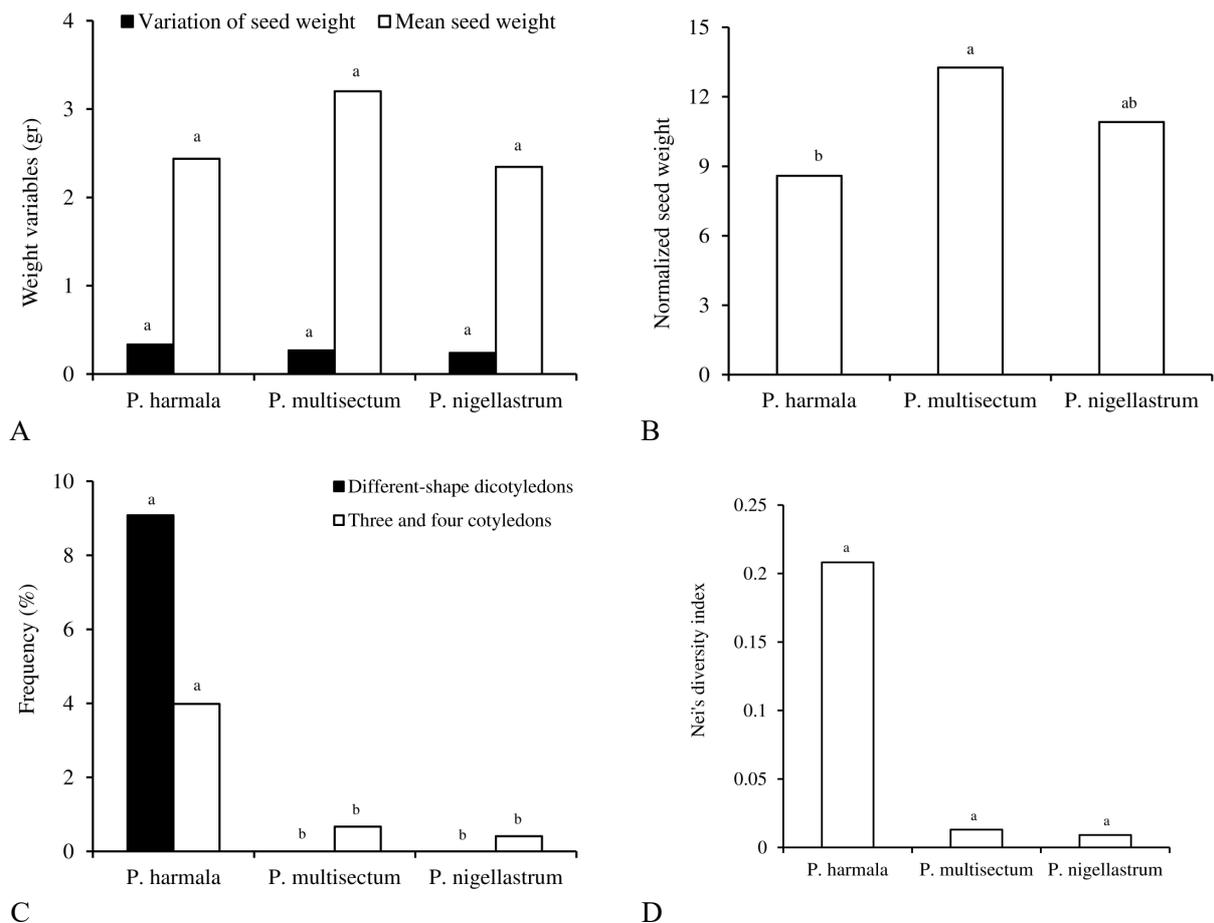


Figure 3. Comparison of the seed weight variation. A – mean seed weight, B – normalized seed weight, C – seedling morphology, D – Nei's diversity index between three species of *Peganum* L. Different letters show significant difference, according to Tukey's Post Hoc test ($P < 0.05$).

Variation of seed weight is negatively correlated with aridity index ($R_s = -0.57$, $P = 0.01$), but it was not significant with precipitation amount ($R_s = -0.41$, $P = 0.09$). ANOVA results showed that variation of seed weight corresponded with aridity index and precipitation amount, suggesting variation of seed weight might differently respond to aridity index and precipitation amount (Fig. 4A & B). Correspondence between variation of seed weight and air temperature was insignificant (Fig. 4C). One site with highest aridity index showed lowest mean seed weight, while one site with lower aridity index showed highest mean seed weight (Fig. 5A). Mean seed weight did not change with precipitation and air temperature (Fig. 5B, C). Low and high normalized seed weight corresponded to low aridity index and precipitation and intermediate normalized seed weight to high aridity index and precipitation. Normalized seed weight increased

with increasing aridity index and precipitation in most sites, but high normalized seed weight corresponded to low aridity index and precipitation in 1, 2 and 1 sites of *P. harmala*, *P. multisectum* and *P. nigellastrum*, respectively (Fig. 6A, B). Correspondence of normalized seed weight with air temperature was insignificant (Fig. 6C). Six sites with high variation of seed weight in *P. harmala* associated to low aridity index and precipitation, but two sites with low variation of seed weight to low and high aridity index. Seven sites with high variation of seed weight in *P. nigellastrum* associated to high aridity index and precipitation, whereas two sites with low and high variations of seed weight to low aridity index. One site with high mean seed weight in *P. multisectum* associated to lower aridity index and precipitation.

Across species, correspondence of variation of seed weight and mean seed weight with Nei's diversity index was insignificant (one

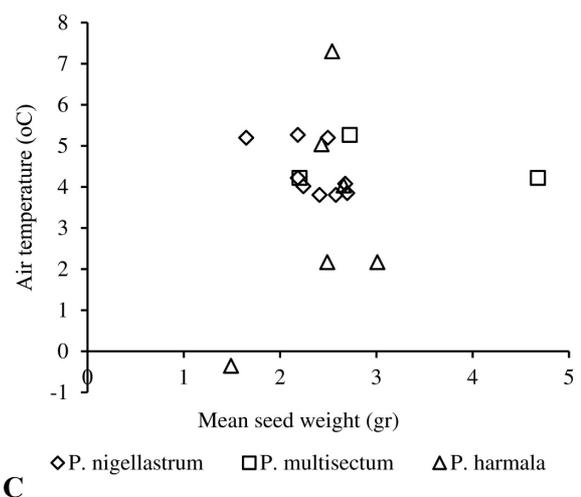
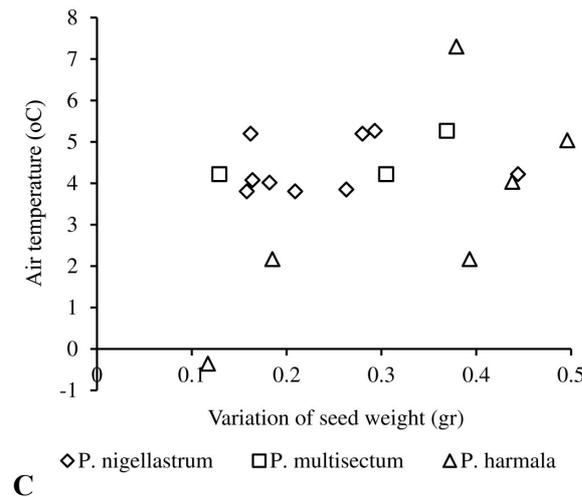
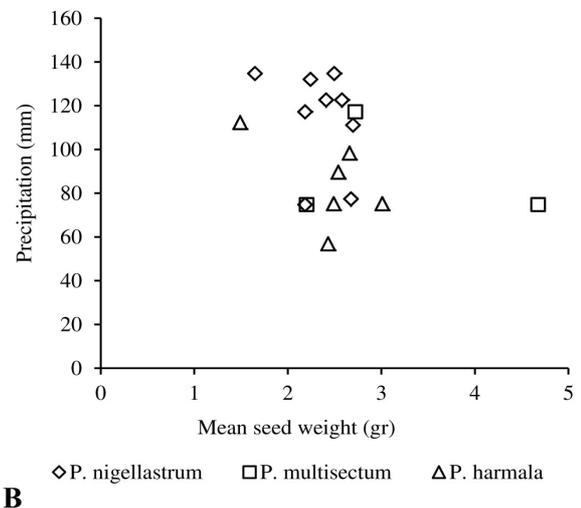
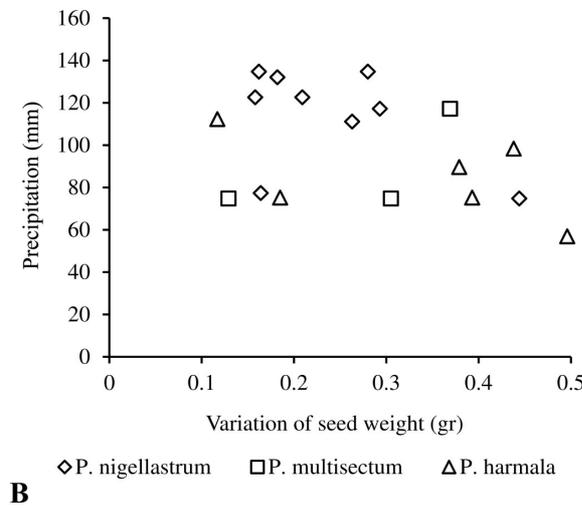
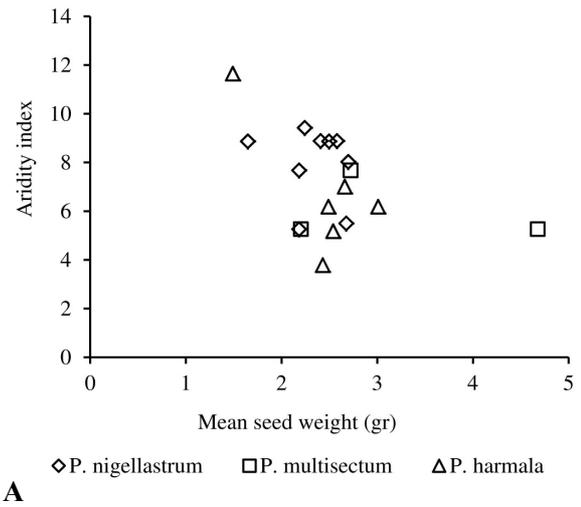
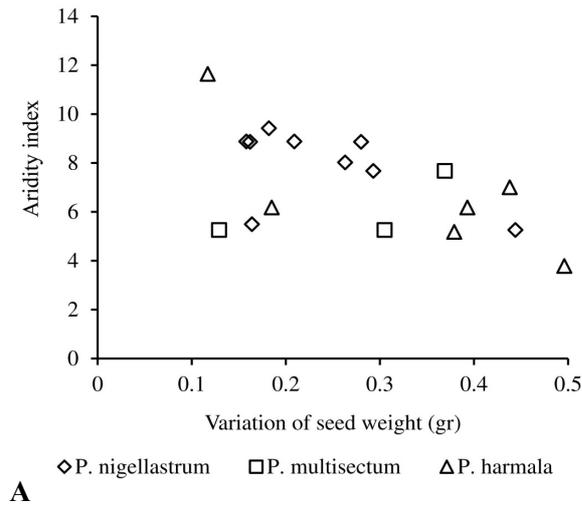


Figure 4. Correspondence between variation of seed weight and climatic factors. A – aridity index ($df=1$, $SS=23.51$, $MS=23.51$, $F=8.26$, $P=0.01$); B – precipitation ($df=1$, $SS=3025.66$, $MS=3025.66$, $F=6.11$, $P=0.02$); C – air temperature ($df=1$, $SS=3.14$, $MS=3.14$, $F=1.23$, $P=0.28$).

Figure 5. Correspondence between mean seed weight and climatic factors. A – aridity index ($df=2$, $SS=23.48$, $MS=11.89$, $F=3.94$, $P=0.04$); B – precipitation ($df=2$, $SS=2357.87$, $MS=1178.93$, $F=2.06$, $P=0.16$); C – air temperature ($df=2$, $SS=8.96$, $MS=4.48$, $F=1.93$, $P=0.18$).

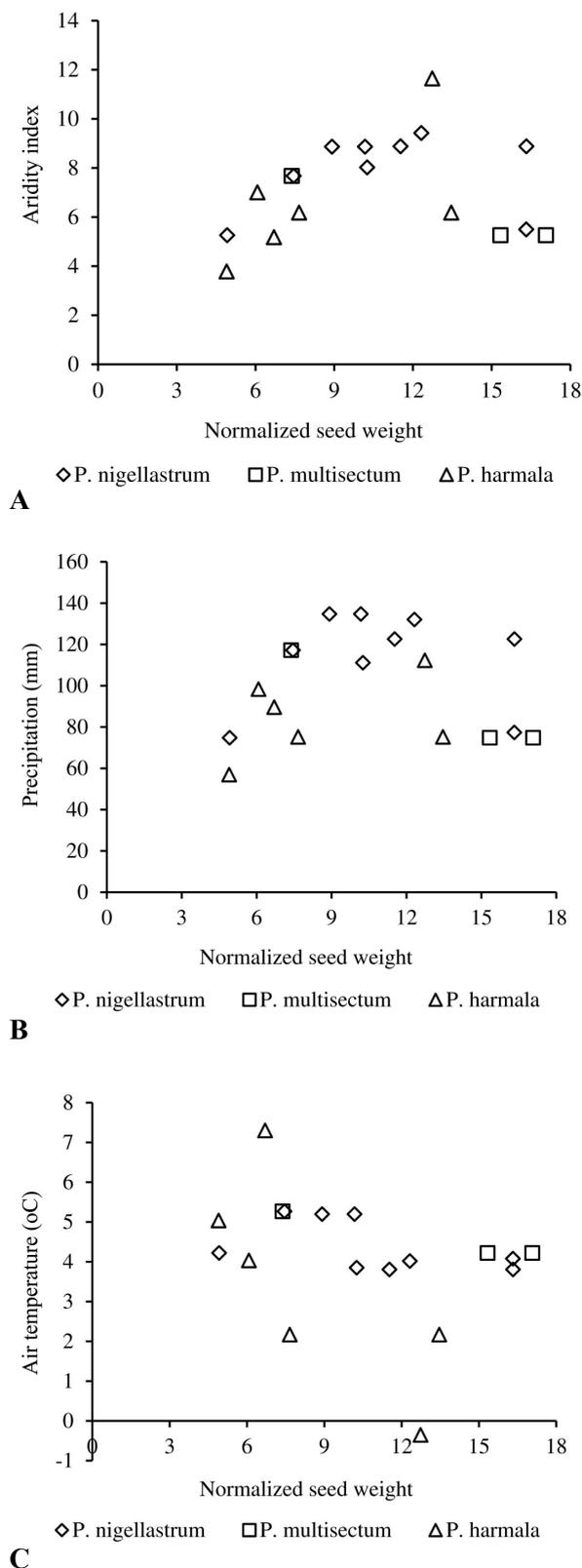


Figure 6. Correspondence between normalized seed weight and climatic factors. A – aridity index ($df=2$, $SS=39.23$, $MS=19.61$, $F=9.86$, $P=0.002$); B – precipitation ($df=2$, $SS=5477.0$, $MS=2738.5$, $F=7.51$, $P=0.005$); C – air temperature ($df=2$, $SS=5.21$, $MS=2.6$, $F=1.01$, $P=0.39$).

way ANOVA, $P=0.07$ and $P=0.11$). Low and high normalized seed weight significantly corresponded with high and low Nei's diversity index (one way ANOVA, $P=0.01$). Within *P. harmala*, low and high variation of seed weight corresponded to low and high Nei's diversity index (Fig. 7A) while low and high normalized seed weight to high and low Nei's diversity index (Fig. 7C). Mean seed weight did not change significantly with Nei's diversity index (Fig. 7B). Within *P. multisectum* and *P. nigellastrum*, low and high mean seed weight significantly corresponded to low and high Nei's diversity index (Fig. 7E), whereas variation of seed weight and normalized seed weight showed insignificance (Fig. 7D, 7F).

Low and high Nei's diversity indices significantly corresponded to high and low aridity index and precipitation (Fig. 8A & 8B), but it showed insignificance with air temperature (Fig. 8C). Seeds of *P. harmala* with high Nei's diversity index were found in sites with low aridity index and precipitation, while those of other species with low Nei's diversity index were in sites with high aridity index and precipitation.

Discussion

As stated by Liu *et al.* (2015) that fruit wall may affect seed weight by regulating the accumulation of photosynthesis. Present results suggest that the accumulation of photosynthesis might affect seed weight of big populations, while cotyledon number and shape of embryo contribute to seed weight of small populations.

Previously, negative (Meyer, 1997; Harel *et al.*, 2011) and positive relationships (Busso & Perryman, 2005; Moles *et al.*, 2005) were found between mean seed weight and climatic aridity, precipitation and air temperature. High variation of seed weight in *P. harmala* was mostly associated to high climatic aridity and low precipitation, but rarely, low variation of seed weight to high and low climatic aridity, while high variation of seed weight in *P. nigellastrum* mostly associated to low climatic aridity and higher precipitation, whereas rarely, low and high variation of seed weight to high climatic aridity. This correspondence showed that variation of seed weight within species differently responds to aridity.

Busso and Perryman (2005) found positive

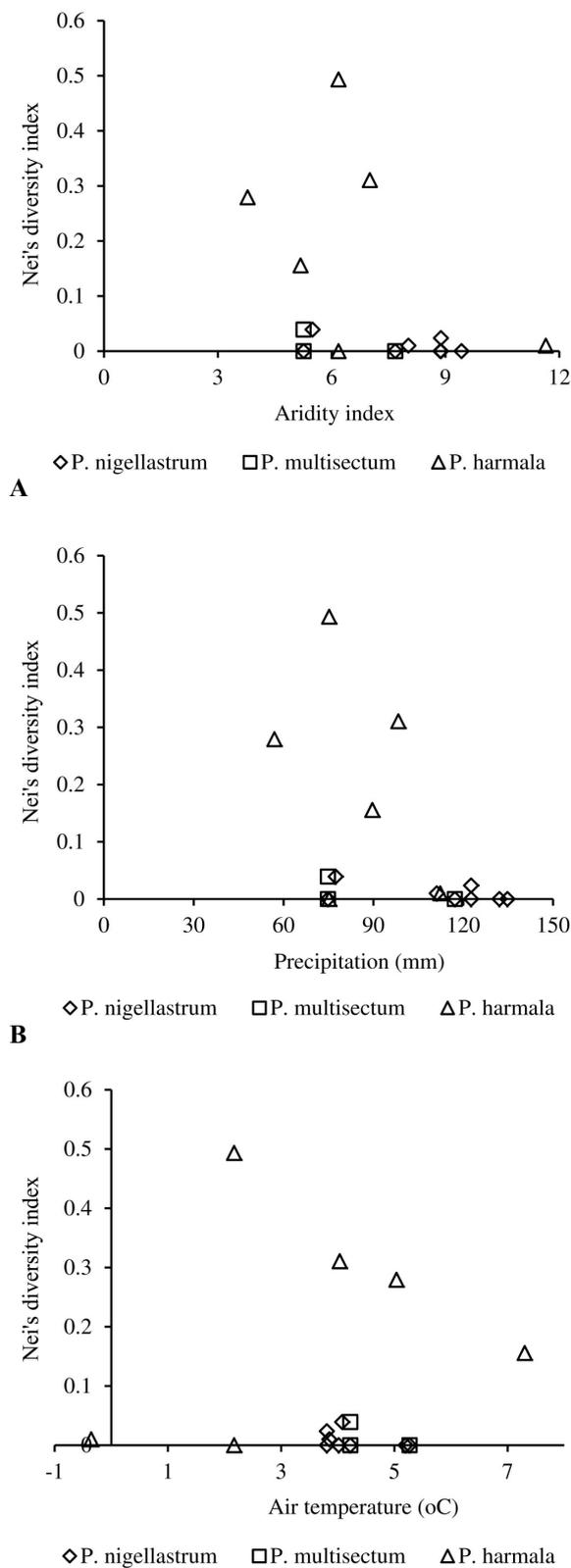


Fig. 8. Correspondence between climatic factors and genetic diversity of three species of *Peganum*. A – aridity index ($df=1$, $SS=0.09$, $MS=0.09$, $F=5.7$, $P=0.03$); B – precipitation ($df=1$, $SS=0.09$, $MS=0.09$, $F=5.7$, $P=0.03$); C – air temperature ($df=5$, $SS=0.08$, $MS=0.02$, $F=0.78$, $P=0.58$).

relationship between mean seed weight and precipitation. The present results revealed that mean seed weight was lowest with lowest climatic aridity, showing low aridity called low mean seed weight. Highest mean seed weight of *P. multisectum* in higher arid site show that mean seed weight increases with increasing aridity.

Seeds of *P. harmala* and *P. multisectum* disperse by only human activities and water flow, while those of *P. nigellastrum* by both wind and human activities (Amartuvshin *et al.*, 2006). Normalized seed weight was lowest in human-dispersal species and highest in hydro-dispersal species, but it was moderate in wind-human-dispersal species, suggesting normalized seed weight may contribute to seed dispersal syndrome.

Seed weight is quantitatively determined mainly by additive gene action (Doganlar *et al.*, 2000). More than two cotyledons and different-shape dicotyledons were found in *P. harmala*, indicating higher gene diversity of cotyledons in *P. harmala*. Within *P. harmala*, variation of seed weight and normalized seed weight corresponded with genetic diversity, resulting in increasing diversity of additive gene. Within *P. multisectum* and *P. nigellastrum*, mean seed weight corresponded with genetic diversity, resulting in non-additive gene diversity (dominant gene diversity). Results on chloroplast DNA sequence showed that a major deletion event occurred in *P. harmala* and more insertion than deletion occurred in *P. multisectum*, but substitution in *P. nigellastrum* (Zhao *et al.*, 2011). In this case, low normalized seed weight associate to species with low genetic diversity while high normalized seed weight to high one.

Researchers suggested that *P. harmala* is older than *P. multisectum* and *P. nigellastrum* (Iljin, 1958), and genetic diversity of *P. harmala* is poorer than other species (Zhao *et al.*, 2011). Population size of *P. harmala* is smaller than other two species in Mongolia. The frequency of more than two cotyledons was highest in species with small population size, suggesting effects of genetic drift (Narantsetseg, 2012). As reported by Hosseini *et al.* (2013) the mean seed weight is higher in polyploidy plants. Present results showed that normalized seed weight was low in species with human-dispersal syndrome, small population size and poor genetic diversity, but it was high in species with water- and wind-

human-dispersal syndromes, with big population size and rich genetic diversity. Also, normalized seed weight was highest in *P. multisectum*, indicating it might be polyploidy species.

Some researchers discussed the interactions between seed weight, genetic divergence and environmental factors, such as climatic aridity (Meyer, 1997; Konarzewski *et al.*, 2012). Present results suggest that variation of seed weight was related with precipitation, climatic aridity and genetic diversity within species. Mean seed weight was related with climatic aridity and genetic diversity within species, but normalized seed weight was related with precipitation, climatic aridity and genetic diversity inter- and within species, suggesting normalized seed weight might contribute to evolution of seed weight.

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