SEED TRAITS OF FIVE ACACIA SPECIES IN TWO AREAS OF SAUDI ARABIA

THOBAYET S. ALSHAHRANI

Plant Production Department, College of Food and Agricultural Sciences, King Saud University, P.O. Box 2460, Riyadh, 11451, Saudi Arabia Corresponding email: talshahrani@ksu.edu.sa, thobayet@yahoo.com

Abstract

This study was conducted to assess the variability of seed traits in homologous pairs of five Acacia species, i.e., *A. asak, A. ehrenbergiana, A. etbaica, A. gerrardii* and *A. origena*, which are naturally distributed in two areas of Saudi Arabia: Asser and Al Baha. Seed traits included length, width, thickness, volume, seed coat thickness and weight, and endosperm weight. The number of intact, infected, and decomposed seeds in the soil were determined too.

Significant spatial differences were observed regarding seed volume, seed coat thickness and infected seeds; these three traits were higher in Asser. The widths of *A. asak, A. ehrenbergiana, A. etbaica,* and *A. gerrardii* seeds were significantly different between the two locations, with higher values found in Asser. Significant differences in the number of decomposed seeds were found for *A. asak, A. etbaica, A. gerrardii* and *A. origena*. Significant variations in seed length were found for *A. asak, A. etbaica, and A. origena;* the seeds tended to be longer in Asser. Seed thickness varied significantly for *A. asak, A. etbaica,* and *A. origena;* the seeds tended to have thicker seeds in Asser. The total seed weight was significantly different for *A. ehrenbergiana, A. etbaica* and *A. origena. Acacia etbaica* and *A. origena* seeds were heavier in Al Baha. The numbers of intact *A. ehrenbergiana, A. etbaica* and *A. origena* seeds were significantly different. Furthermore, the endosperm weight varied significantly for *A. etbaica* and *A. origena* with higher weights being observed in Al Baha. The seed coat weight varied only in *A. origena*.

Key words: Asser, Al Baha, Acacia, seeds, Saudi Arabia.

Introduction

In plant species, seed biology is among the most relevant research topics because of its role in plant establishment, succession and natural regeneration (Janzen & Vázquez-Yanes, 1990; Vázquez-Yanes & Orozco-Segovia, 1993). Seed size (mass) affects various aspects of plant life, such as dispersal, establishment, emergence, seed water relation, survival and seedling growth (Milberg & Lomant, 1997). Variations in seed mass are primarily observed within families or genera (Wolfe, 1995) and between populations of widespread species (Cavers & Steel, 1984). However, the seed mass within a species is considered to be a remarkably constant characteristic (Bu et al., 2007), and the seed mass is similar in closed, related species regardless of ecological factors (Wang et al., 2014). Variation in seed traits (e.g., width, length and thickness) is the consequence of a compromise between the need for dispersal (which favors small seeds) and the requirements for establishment seedlings (which favors large seeds); and large seeds positively affect seedling survival rate (Wang et al., 2017). The performance of seeds under different environmental conditions is associated with the physical, chemical, morphological and anatomic properties of the seed coat; these properties vary among species (Souza & Marcos-Filho, 2001). Seed coat morphology is less affected by the environmental conditions under which a plant grows (Wada & Reed, 2008; Gandhi et al., 2011). Souza & Marcos-Filho (2001) concluded that seed susceptibility to mechanical damage depends on the lignin content of the seed coat and that seed coat integrity enhances seed resistance to field weathering. Seed trait variations with respect to seed length, width and weight have previously been reported in several species, such as Cordia african (Loha et al., 2006), Albizzia lebbek (Bhat & Chauhan, 2002), and Pongamia pinnata (Shivanna et al., 2007). Seed size is affected by genetic traits, plant height, growth form, dispersal mode, shade, environmental stresses, geographic location, climate and soil texture (Harper et al., 1970; Leishman et al., 2000; Schmidt, 2000; Membrives et al., 2003).

Seed source testing of native trees is preferable for understanding spatial variations and for selecting the best provenance of a desired species within a specific region to achieve maximum productivity in plantation forestry (Takuathung *et al.*, 2012). The purpose of this study was to determine whether seeds of five acacia species distributed in two separate areas displayed differences in their morphological seed traits (e.g., thickness, mass and size) and species soil seed bank properties (e.g., intact, infected, broken and decomposed seeds).

Material and Methods

Study area: This study was conducted in two areas separated by 380 km: Asser and Al Baha (Fig. 1). Acacia species are naturally distributed with a high density in regions with optimal climate conditions for growth (Fig. 2).

Seed collection: Acacia asak (Forssk) Willd, A. ehrenbergiana (Hayne), A. etbaica (Schweinf), A. gerrardii (Benth) and A. origena are naturally distributed in the Al Baha and Asser areas of Saudi Arabia. However, the selection of sampling plots was based on species distribution, density, and topography. In each sample plot, four trees per species were randomly chosen for seed bank analysis. A total of nine quadrats (0.5 X 0.5 m) were laid at the canopy of individual tree species. Inside each quadrat, a soil sample for each individual was collected at a depth of 5 cm and saved in a fabric bag. Later, the soil samples were sieved using 3, 5 and 8 mm meshes to remove stones, soil and other debris. Then, the seeds in each sample were counted and categorized into four groups: intact seeds, insect-infested seeds (infected), broken seeds, and partially decomposed seeds. After scarification with sandy paper, the intact seeds were germinated at 25°C in Petri dishes with 10 seeds per dish and 4 replicates. Seeds were considered to be germinated when emerging radicals were elongated to 1 mm.

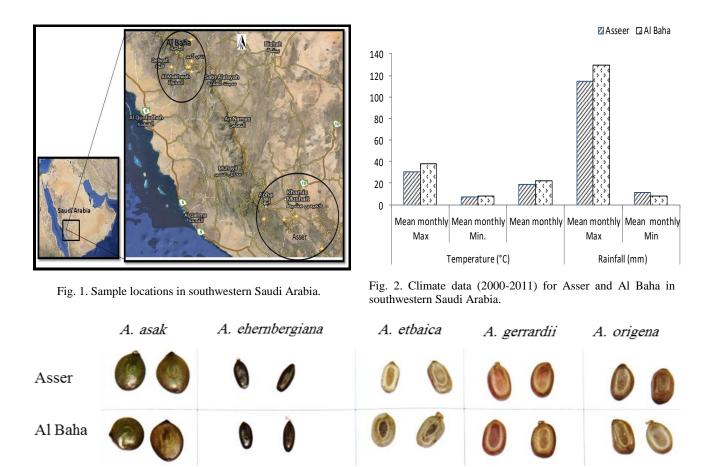


Fig. 3. Seeds of five Acacia species growing in two regions of southwestern Saudi Arabia.

To determine the seed traits, mature seeds for each species were collected from different individuals in both regions (Fig. 3). For each species, fifty seeds were measured for their individual length (L, longest axis), width (W, intermediate axis) and thickness (T, shortest axis) using a digital caliper. These seed dimensions were used to calculate the seed volume according to Cerda & Garcia-Fayos (2002). To measure the seed coat thickness and endosperm weight, 30 seeds of each species were immersed in water at room temperature for 72 h. A small hand-held sharp cutter was used to carefully split the seed coats into two equal halves without damaging the endosperm. The seed coat was subsequently separated from the endosperm. The endosperm and seed coat were immediately dried at room temperature for 120 h; the dry weight was measured using a digital scale. The seed coat thickness was measured using one of the halves with a digital caliper.

Statistical analysis: The collected data were subjected to analysis of variance (two-way ANOVA) using SAS 9.1 for Windows; multiple comparison tests were used to investigate the differences between means at p<0.05.

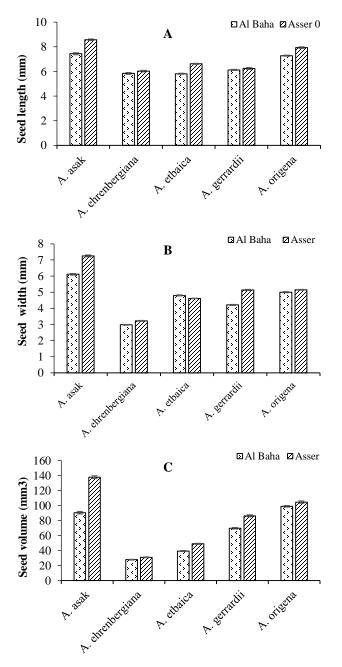
Results

The region, species and their interaction had a significant effect on the observed seed traits. However, the results below show only the interaction of these two factors.

The seed length varied significantly between acacia species ($p \le 0.0001$). There were significant differences in the seed length between seeds from Asser and Al Baha for

A. asak, A. ehrenbergiana, A. etbaica and A. origena. On average, the seeds from Asser were longer (Fig. 4A). Additionally, highly significant differences in the seed width were also observed ($p \le 0.0001$). A. asak trees in Asser had wider seeds than the same species in Al Baha, which was also true for A. ehrenbergiana and A. gerrardii (Fig. 4B). The differences in the seed volume between species were highly significant for all acacia species ($p \le 0.0001$). Furthermore, the results showed that seed volume for all acacia species in Al Baha (Fig. 4C).

The seed thickness varied significantly between the studied acacia species ($p \le 0.009$). The mean seed thicknesses of A. Asak and A. etbaica seeds in Asser were significantly different than the seeds collected in Al Baha. The A. origena seeds collected in Al Baha were significantly thicker than those obtained in Asser (Fig. 5A). The endosperm weight varied significantly between the studied acacia species ($p \le 0.008$). The endosperm weights of A. etbaica and A. origena seeds in Al Baha were significantly different compared with the seeds of the same species in Asser (Fig. 5B). Based on these results, significant differences between the studied acacia species regarding seed coat weight were found $(p \le 0.046)$. The only species with a significant difference in the seed coat weight between seeds from the different locations was A. origena (Fig. 5C). No significant differences in the seed coat weight between the two regions were observed for A. asak, A. ehrenbergiana, A. etbaica or A. gerrardii seeds (Fig. 5C).



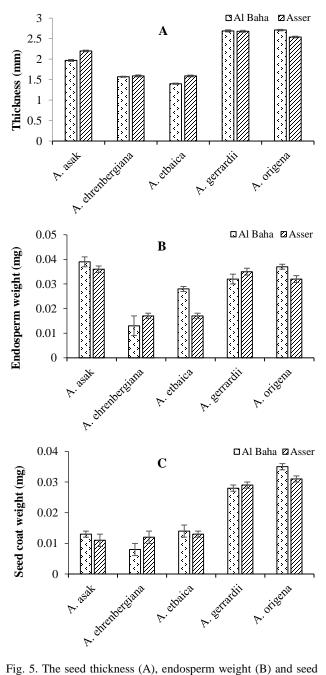
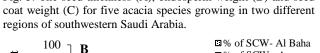
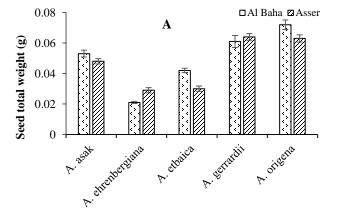


Fig .4 The seed length (A), width (B) and volume (C) for five acacia species growing in two different regions of southwestern Saudi Arabia.





□% of SCW- Al Baha □% of SCW- Asser B Percentage of seed coat weifg □% of ENW- Al Baha 80 60

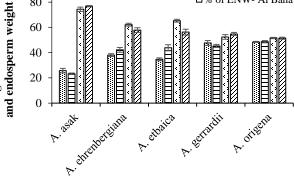
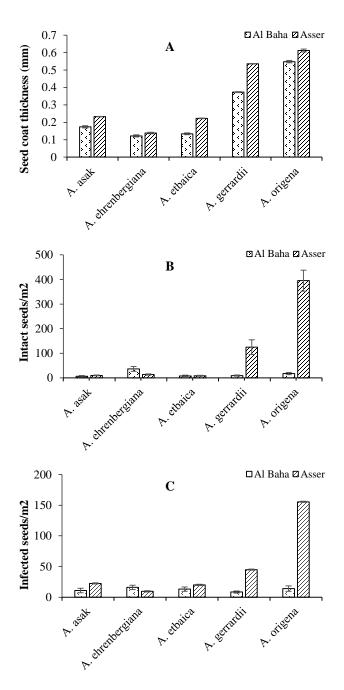


Fig. .6 The percentage of the seed coat weight (A) and endosperm weight to the total seed weight (B) for five acacia species growing in two regions of southwestern Saudi Arabia.

1534



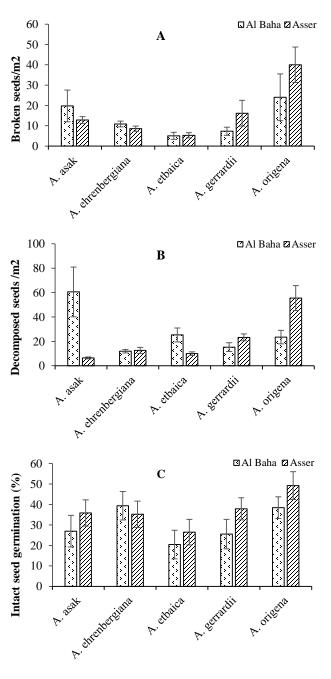


Fig. .7 The seed coat thickness (A), number of intact seeds (B), and number of infected seeds (C) for five acacia species growing in two different regions of southwestern Saudi Arabia.

Significant differences were observed in the total seed weight ($p \le 0.0008$). The mean total seed weight of *A. origena* and *A. etbaica* seeds collected in Al Baha exceeded the weight of the seeds sampled in Asser, although the *A. ehrenbergiana* seeds from Asser had a higher total seed weight compared with the same species in Al Baha (Fig. 6A). Significant variations in the percentage of the endosperm weight ($p \le 0.008$) and seed coat weight ($p \le 0.006$) to the total seed weight was observed. The percentage of the endosperm weight in *A. etbaica* and *A. ehrenbergiana* was significantly higher in Al Baha compared with the same species in Asser; the opposite result was found for the seed coat weight (Fig. 6B). Additionally, the endosperm weight percentage for *A.*

Fig. 8. The number of broken seeds (A), decomposed seeds (B) and the intact seed germination percentage (C) for five acacia species growing in two different regions of southwestern Saudi Arabia.

asak was higher in Asser than in Al Baha; the opposite was true for the seed coat weight percentage (Fig. 6B).

The seed coat thickness varied significantly between the studied species ($p \le 0.0004$). Significant differences were observed in all five acacia species when comparing the mean seed coat thicknesses observed in the two areas. The seed coats from the acacia species in Asser were thicker than those observed in Al Baha (Fig. 7A). The difference in the number of intact seeds in the soil was highly significant ($p \le 0.0001$). The data showed significant spatial differences in the number of intact seeds/m² for *A. ehrenbergiana*, *A. gerrardii* and *A. origena* (Fig. 7B). However, more intact *A. origena* and *A. gerrardii* seeds were found in Asser than in Al Baha, although there were more intact *A. ehrenbergiana* seeds in Al Baha than in Asser (Fig. 7B).

			Seed traits					C. J
	Length	Width	Thickness	Volume	Seed coat weight	Endosperm weight	Seed total weight	Seed coat thickness
Sand	-0.3394	-0.1974	-0.3777	-0.3492	-0.5382	-0.3355	-0.4955	-0.5425
	0.0080	0.1305	0.002	0.0062	0.0001	0.008	0.0001	0.0001
Silt	0.1838	0.0654	0.2933	0.1890	0.4736	0.2295	0.4004	0.3841
	0.1596	0.6191	0.0229	0.1481	0.0001	0.0776	0.0015	0.0024
Clay	0.2971	0.1481	0.3886	0.3258	0.5780	0.3558	0.5297	0.6897
	0.0211	0.2586	0.0021	0.0111	0.0001	0.0053	0.0001	0.0001
ОМ	0.1761	0.1526	0.1268	0.1809	0.2642	0.1233	0.2208	.0.3412
	0.1782	0.2444	0.3341	0.1665	0.0413	0.3480	0.0900	0.0076
pН	-0.2208	-0.1637	-0.0750	-0.2178	-0.0085	-0.0709	-0.0454	-0.1535
	0.1358	0.2713	0.6159	0.1412	0.9544	0.6356	0.7615	0.3028
HCO ₃ -	0.0843	0.0393	0.1873	0.1019	0.2636	-0.603	0.1207	0.3028
	0.5215	0.7651	0.1518	0.4381	0.0418	0.6470	0.3579	0.0187
Cl^{-} SO_4^{2-} Ca^{2+} Mg^{2+} Na^+	-0.3260	-0.2460	0.0714	-0.2415	0.1147	0.0707	0.1052	-0.1156
	0.0110	0.0580	0.5872	0.0630	0.3827	0.5911	0.4237	0.3789
. SO4 ²⁻	-0.4269	-0.3374	-0.0512	-0.3521	0.0095	-0.0714	-0.0332	-0.1638
	0.0007	0.0084	0.6976	0.0058	0.9424	0.5873	0.8009	0.2109
Ca^{2+}	-0.2972	-0.3690	0.0698	-0.2777	0.0484	-0.0898	-0.0205	-0.1233
<u>.</u>	0.0211	0.0037	0.5961	0.0317	0.7134	0.4948	0.8759	0.3477
$\frac{1}{2}$ Mg ²	-0.1320	-0.1046	0.0550	-0.0744	0.1492	-0.0050	0.0841	0.1103
	0.3146	0.4261	0.6762	0.5717	0.2551	0.9694	0.5226	0.4011
Na ⁺	-0.2669	-0.1921	0.2013	-0.1349	0.0775	0.0983	0.0985	-0.0219
	0.0392	0.1413	0.1230	0.3041	0.5559	0.4548	0.4539	0.8680
N	-0.0355	-0.0346	0.3453	0.0749	0.3913	0.2072	0.3404	0.2097
•	0.7874	0.7929	0.0069	0.5694	0.0020	0.1121	0.0078	0.1077
Г	-0.2635	-0.1590	0.0372	-0.1876	-0.0232	-0.0055	-0.0165	-0.2007
	0.0419	0.2249	0.7774	0.1510	0.8601	0.9667	0.9003	0.1240
\mathbf{K}^+	-0.3143	-0.1032	0.1400	-0.1538	0.0101	-0.1654	-0.0839	-0.1951
	0.0144	0.4323	0.2859	0.2405	0.9389	0.2064	0.5237	0.1351
Fe	0.0767	0.0478	0.2556	0.1574	0.3307	0.2289	0.3169	0.3268
	0.5599	0.7168	0.0487	0.2295	0.0098	0.0784	0.0136	0.0108
Mn	-0.0626	0.0259	-0.0569	-0.0639	0.1040	0.1164	0.2579	-0.0370
	0.6345	0.8439	0.6655	0.6273	0.4289	0.3755	0.0466	0.7787
Zn	0.2362	0.2208	0.4207	0.3547	-0.2195	-0.2721	-0.0860	-0.1085
	0.0692	0.0900	0.0008	0.0054	0.0919	0.0354	0.5134	0.4090
Cu	0.2016	0.1687	0.3998	0.2973	-0.1554	-0.1800	-0.0581	-0.1163
	0.1224	0.1973	0.0016	0.0211	0.2357	0.1687	0.6590	0.3760

Table 1. Pearson's correlation coefficients with *p*-values (italic) for relationships between seeds traits and soil properties.

Bold indicates significant correlation at p<0.05

The difference in the number of infected seeds was highly significant ($p \le 0.0001$). The results demonstrated significant regional differences in the number of infected seeds/m² for A. asak, A. ehrenbergiana, A. etbaica, A. gerrardii and A. origena; the number of infected seeds was higher in Asser for all species except A. ehrenbergiana (Fig. 7C). With respect to broken seeds, the regional difference was not significant (P=0.1793, Fig. 8A), although the difference in decomposed seeds/m² was highly significant $(p \le 0.0001)$. The number of decomposed A. origena and A. gerrardii seeds was higher in Asser than Al Baha, although the number of decomposed A. asak and A. etbaica seeds was higher in Al Baha than Asser (Fig. 8B). The interaction between region and species was found to exhibit no significant effect on the intact seed germination percentage (P=0.0566). The highest germination percentage was observed for A. origena in Asser, although the result was not significantly different from A. origena in Al Baha (Fig. 8C).

Discussion

In the current study, Acacia species were found to exhibit regional differences in the observed mean seed traits. The differences in the Acacia seed traits could be related to species growing in areas with a wide range of altitudes (150-2700 m), rainfall amounts (120-500 mm) and temperatures (25-42°C). Differences in the seed mass within a species have been reported for many plant species (Schaal, 1980; Cordazzo, 2002). Abdelkheir et al., (2003) found that geographical sources of Acacia karoo had a significant effect on seed weight, seed length, width and thickness. Kumar et al., (2007) demonstrated that variations in cone and seed characteristics may appear if stands are far apart or if there is some geographic barrier between them. The seed mass has been reported to decrease with elevation in Sorbus aucuparia (Barclay & Crawford, 1984) and Picea abies; (Oleksyn et al., 1998).

However, previous work has shown that the seed weight in *Betula pubescens* increases with altitude (Holm, 1994), although the seed mass within a species can vary. The results of this study demonstrate that the seed mass variations between acacia species are consistent with the results of Schaal (1980) and Cordazzo (2002).

Additionally, the soil can play a significant role in seed trait variations; some morphological traits evolve in association with soil texture (Membrives *et al.*, 2003). In Sudan, Raddad (2007) found that *A. Senegal* provenances grown in clay plains had lighter seeds, whereas sand plain provenances had heavier seeds. Hammond & Brown (1995) also found no significant relationship between soil type and seed size in Neotropical woody species. Thus, highly variable soil moisture may play a more determinant role in seed output than soil type. Wen *et al.*, (2014) found that the seed weight and oil content of *J. curcas* grown in acidic soil types were higher when compared with the same species grown in calcium soil types.

Rosa et al., (2014) found that organic matter only explained seed mass variations. Organic matter reserves nitrogen and contributes to chemical and biological processes that are directly related to productivity (Craswell & Lefroy, 2001). In this study, organic matter variations do not explain the total seed weight variations because no significant correlation was found between the two variables (r=0.0900, p=0.2208). Dainese & Sitzia (2013) demonstrated that soil fertility was the most important predictor for seed mass variations in mountain grasslands. Dainese & Sitzia (2013) also reported that the seed mass in low-fertility soil was higher than for plants in high-fertility soil. Therefore, higher seed masses in drier or nutrient-poor environmental conditions may act as a buffer against devastating conditions (Leishman & Westoby, 1994; Wright & Westoby, 1999). The relationship between seed size and soil nutrient availability remains unclear. Lee & Fenner (1989) reported that large seeds were associated with low-fertility soil in 12 species of Chionochloa in New Zealand. The same association was reported for two species pairs in the Proteaceae (Mustart & Cowling, 1992). By contrast, Grubb & Coomes (1997) found that smaller mean seed sizes were associated with poorer soil conditions in 27 Amazonia forest species. However, the seed mass, expressed as the total seed weight, was high in species grow in soil with low P contents (A. asak and A. origena in Al Baha and A. gerrardii in Asser) (Table 1 and Fig. 6A), although no significant correlation was found between P and the total seed weight (r=0.01652, p=0.9003). Other studies have also failed to determine a relationship between the seed size and soil type for various species (Westoby et al., 1990; Hammond & Brown, 1995; Wright & Westoby, 1999).

Funes *et al.*, (2003) found that seed bank richness and density increase with altitude. Whereas a cold climate at high elevations may favor the formation of a persistent seed bank, the relatively warm conditions at lower elevations may increase the activity of seed predators. In *A. origena* in Asser, where the species occupies elevations exceeding 2500 m, the number of intact and infected seeds/m² was high (450 and 160, respectively). However, for species like *A. asak*, which are found at low elevations (i.e., 150 m), the number

of infected seeds was 30 seed/m². The effects of elevation on biotic and abiotic factors may explain the differences in the number of intact and infected seeds and plant productivity. Previous research has shown that some host plants become more susceptible to fungi and rust diseases and insect predation at higher temperatures (Hunter, 2001). However, it is often assumed that the variability in seed traits, especially the endosperm weight, which was reported in this study, may influence the choice of seed predators, especially insects; this assumption appears to be true based on the number of infected A. origena seeds in Asser. Additionally, numerous decomposed A. origena seeds could be a result of increased soil moisture. Soil moisture enhances fungal infection and predation of seeds (Funes et al., 2003). Abdullah & Abulfatih (1994) studied the distribution of Acacia trees and bruchid seed beetles in southwestern Saudi Arabia and found that each host-insect pair occupied a specific range along the altitudinal gradient from sea level to 2500 m. At altitudes between sea level and 1750 m, Acacia asak was the host for Bruchidius sp, whereas A. ehrenbergiana hosted B. saudicus. At higher altitudes (between 1750 and 2500 m), A. origena hosted B. arabicus, whereas and A. gerrardii was the host of B. arabicus. However, variations in the number of infected seeds may reflect the ability of a species to produce secondary defense compounds. Acacia tree seeds accumulate nonprotein amino acids as secondary compounds (Evans et al., 1993); these compounds may provide insect deterrence, toxicity, and phytotoxicity (Romeo, 1998). However, long seed persistence is a trade-off between investments in physical or chemical seed protection. Tiansawat et al., (2014) demonstrated that variations in seed defense with prolonged soil persistence depended primarily on physical rather than chemical seed defense. Seed susceptibility to mechanical damage depends on the lignin content of seed coats, and seed coat integrity enhances seed resistance to field weathering (Souza & Marcos-Filho, 2001).

Variations in seed morphometric traits may also be the result of the adaptation to diverse environmental conditions. In plant, morpho-anatomical and structural trait diversity seems to be related to an environmental complexity (Kuzminsky et al., 2014). In addition to environmental factors, genetic components contribute strongly to variations in the seed mass. Variations in seed traits (e.g., width, length and thickness) represent a compromise between the necessity for dispersal, which favors small seeds, and the requirements for establishing seedlings, which favors large seeds. Seed coat morphology is less affected by environmental conditions under which a plant grows (Hong et al., 1999, Abdel-Khalik, 2006; Wada & Reed, 2008; Gontcharova et al., 2009; Gandhi et al., 2011). Large seeds have relatively heavier seed coats (Fenner, 2012) because large seeds are more easily exposed to surface predators (Van Oudtshoorn & Van Rooyen, 1999). The size of small seeds enhances the buildup of the soil seed bank. Undoubtedly, small seeds are more capable of reducing insect attacks because they cannot support the development of a bruchid larva (Thompson, 1987). Furthermore, heavier seeds produce seedlings that can resist environmental hazards and support environmental resistance mechanisms (Leishman & Westoby, 1994).

Conclusion

The study revealed variations in seed traits between the same species of acacia in the two areas. The observed values for most of the studied seed traits in Asser exceed those for Al Baha. These differences may be due to the effects of both environmental and genetic variations. More research is required to determine seed chemical defenses and to explain the variations between species of intact and infected seeds.

Acknowledgment

The authors thank the College of Food and Agricultural Research Center and the Deanship of Scientific Research, King Saud University, Saudi Arabia for supporting this work.

References

- Abdel–Khalik, K.N. 2006. Seed morphology of *Cuscuta L.* (Convolvulaceae) in Egypt and its systematic significance. *Feddes Repertorium*, 117: 217-224.
- Abdelkheir, R.M., A. Ibrahim and A. Khali. 2003. Provenance variation in seed and germination characteristics of *Acacia karo*. *Sudan Silva*, 9(2): 14- 26.
- Abdullah, M.A. and H.A. Abulfatih. 1994. Predation of Acacia seeds by bruchid beetles and its relation to altitudinal gradient in south-western Saudi Arabia. *J. Egypt Soc. Parasitol.*, 24(1): 107-119.
- Barclay, A.M. and R.M. Crawford. 1984. Seedling emergence in the rowan (*Sorbus aucuparia*) from an altitudinal gradient. J. *Ecol.*, 72: 627-636.
- Bhat, G.H. and P.S. Chauhan. 2002. Provenance variation in seed and seedling traits of *Albizzia lebbek* Benth. J. Tree Sci., 21: 52-57.
- Bu, H., X. Chen, X. Xu, K. Liu, P. Jia and G. Du. 2007. Seed mass and germination in an alpine meadow on the eastern Tsinghai-Tibet plateau. *Plant Ecol.*, 191: 127-149.
- Cavers, P.B. and M.G. Steel. 1984. Patterns of change in seed weights over time on individual plants. *Am. Nat.*, 124: 324-335.
- Cerda, A. and P. Garcia-Fayos. 2002. Influence of seed size and shape on their removal by water erosion. *Catena*, 48: 293-301.
- Cordazzo, C.V. 2002. Effect of seed mass on germination and growth in three dominant species in southern brazilian coastal dunes. *Braz. J. Biol.*, 62(3): 427-435.
- Craswell, E.T. and R.D. Lefroy. 2001. The role and function of organic matter in tropical soils. *Nutr. Cycl. Agroecosyst*, 61: 7-18.
- Dainese, M. and T. Sitzia. 2013. Assessing the influence of environmental gradients on seed mass variation in mountain grasslands using a spatial phylogenetic filtering approach. *Perspect. Plant Ecol. Evol. Syst.*, 15: 12-19.
- Evans, C.S., A.J. Shah, M.W. Adlard and R.A. Lourdes. 1993. Non-protein amino acids in seeds of neotropical species of Acacia. *Phytochemistry*, 32: 123-126.
- Fenner, M. 2012: Seed Ecology. Springer.
- Funes, G., S. Basconcelo, S. Díaz and M. Cabido. 2003: Seed bank dynamics in tall-tussock grasslands along an altitudinal gradient. J. Veg. Sci., 14: 253-258.
- Gandhi, D., S. Albert and N. Pandya. 2011. Morphological and micromorphological characterization of some legume seeds from Gujarat. *India. Environ. Exp. Biol.*, 9: 105-113.
- Gontcharova, S.B., A.A. Gontcharov, V.V. Yakubov and K. Kondo. 2009: Seed surface morphology in some representatives of the genus Rhodiola sect. Rhodiola (Crassulaceae) in the Russian Far East. *Flora*, 204: 17-24.

- Grubb, P.J. and D.A. Coomes. 1997. Seed mass and nutrient content in nutrient-starved tropical rainforest in Venezuela. *Seed Sci. Res.*, **7**: 269-280.
- Hammond, D.S. and V.K. Brown. 1995. Seed size of woody plants in relation to disturbance, dispersal, and soil type in wet Neotropical forests. *Ecology*, 76: 2544-2561.
- Harper, J.L., P. H. Lovell and K.G. Moore. 1970. The shapes and sizes of seeds. *Annu. Rev. Ecol. Syst.*, 1: 327-356.
- Holm, S.O. 1994. Reproductive patterns of *Betula pendula* and *B. pubescens* Coll. along a regional altitudinal gradient in northern Sweden. *Ecography*, 17: 60-72.
- Hong, S.P., M.J. Han and K.J. Kim. 1999. Systematic Significance of Seed Coat Morphology in *Silene L. s. str.* (*Sileneae-Caryophyllaceae*) from Korea. *J. Plant Biol.*, 42(2): 146-150.
- Hunter, M.D. 2001. Effects of elevated atmospheric carbon dioxide on insect plant interactions. *Ag Forest Entomol.*, 3: 153-159.
- Janzen, D.H. and C. Vázquez-Yanes. 1990. Aspects of tropical seed ecology of relevance to management of tropical forested wildlands. In: *Rain forest regeneration and management*, (Eds.): Gómez, A.P., T.C. Whitmore and M. Hadley UNESCO and Parthenon, Paris, France, pp. 137-157.
- Kumar, D., S.S. Negi, R. Pandey, I. Pundir, A. Tomar and P. Kumar. 2007. Variation in cone and seed morphology of *Pinus roxburghii*: effect of population and mother tree. *Indian Forester*, 133: 749-757.
- Kuzminsky, E., P. De Angelis, R. Abou Jaoudé, G. Abbruzzese, S. Terzoli, C. Angelaccio, G. De Dato, M.C. Monteverdi and V. Riccardo. 2014. Biodiversity of Italian *Tamarix spp.* populations: Their potential as environmental and productive resources. *Rendiconti Lincei*, 25(4): 439-452.
- Lee, W.G. and M. Fenner. 1989. Mineral nutrient allocation in seeds and shoots of twelve Chionochloa species in relation to soil fertility. J. Ecol., 77: 704-716.
- Leishman, M.R. and M. Westoby. 1994. The role of seed size in seedling establishment in dry soil-conditions experimental evidence from semiarid species. *J. Ecol.*, 82: 249-258.
- Leishman, M.R., I. J. Wright, A.T. Moles and M. Westoby. 2000. The evolutionary ecology of seed size. *In*: (Fenner, M. edt.) *Seeds: The Ecology of Regeneration in Plant Communities*, CABI Pub., NY, pp. 31-58.
- Loha, A., M. Tigabu, D. Teketay, K. Lundkvist and A. Fries. 2006. Provenance variation in seed morphometric traits, germination, and seedling growth of *Cordia africana* Lam. *New Forests*, 32: 71-86.
- Membrives, N., J. Pedrola-Monfort and J. Caujape-Castells. 2003. Correlations between morphological-anatomical leaf characteristics and environmental traits in Southwest African species of Androcymbium (Colchicaceae). *Bot. Macaronesica*, 24: 73-85.
- Milberg, B.P. and B.B. Lamont.1997. Seed/cotyledon size and nutrient content play a major role in early performance of species on nutrient-poor soils. *New Phytol.*, 137: 665-672.
- Mustart, P.J. and R.M. Cowling. 1992. Seed size: Phylogeny and adaptation in two closely related Proteaceae species-pairs. *Oecologia*, 91: 292-295.
- Oleksyn, J., J. Modrzynski, M.G. Tjoelker, R. Zytkowiak, P.B. Reich and P. Karolewskin. 1998. Growth and physiology of Picea abies populations from elevational transects: common garden evidence for altitudinal ecotypes and cold adaptation. *Func. Ecol.*, 12: 573-590.
- Raddad, E.Y. 2007. Ecophysiological and genetic variation in seedling traits and in first-year field performance of eight *Acacia senegal* provenances in the Blue Nile, Sudan. *New Forests*, 34(3): 207-222.
- Romeo, J.T. 1998. Functional multiplicity among nonprotein amino acids in mimosoid legumes: A case against redundancy. *Ecoscience*, 5: 287-294.

- Rosa, R. K., R.I. Barbosa and S. Koptur. 2014. Which factors explain reproductive output of *Mauritia flexuosa* (Arecaceae) in forest and savanna habitats of northern amazonia?. *Int. J. Plant Sci.*, 175(3): 307-318.
- Schaal, B.A. 1980. Reproductive capacity and seed size in *Lupinus texensis. Am. J. Bot.*, 67: 703-709.
- Schmidt, L. 2000. *Guide to handling of tropical and subtropical forest seed*. Danida Forest Seed Centre, Denmark.
- Shivanna, H., H.C. Balachandra and N.L. Suresh. 2007. Source Variation in seed and Seedling Traits of *Pongamia pinnata*. *Karnataka J. Agri. Sci.*, 20: 438-439.
- Souza, F.H.D. and J. Marcos-Filho. 2001. The seed coat as a modulator of seed-environment relationships in Fabaceae. *Rev. Bras. Bot.*, 24 (4): 365-375.
- Takuathung, C.N., D. Pipatwattanakul and S. Bhumibhamo. 2012. Provenance variation in seed morphometric traits and growth performance of *Senna siamea* (Lam.) Erwin et Barneby at Lad Krating Plantation, Chachoengsao Province, Thailand. *Kasetsart. J. Nat. Sci.*, 46: 394-407.
- Thompson, K. 1987. Seeds and seed banks .New Phytol, 106: 23-34 12.
- Tiansawat, P., A.S. Davis, M.A. Berhow, P.C. Zalamea and J.W. Dalling. 2014. Investment in seed physical defense is associated with species' light requirement for regeneration and seed persistence: Evidence from Macaranga species in Borneo. *PLoS ONE*, 9(6): e99691.
- Van Oudtshoorn, K.V. and M.W. Van Rooyen. 1999. Dispersal Biology of Desert Plants. Springer, 1st ed. Berlin, Heidelberg, Germany.

- Vázquez-Yanes, C. and A. Orozco-Segovia. 1993. Pattern of seed longevity and germination in the tropical rain forest. *Annu. Rev. Ecol. Evol. Syst.*, 24: 69-87.
- Wada, S. and B.M. Reed. 2008. Morphological analysis of Rubus seed. Acta Hort., 782: 67-74.
- Wang, T.T., G.M. Chu, P. Jiang, P.X. Niu and M. Wang. 2017. Effects of sand burial and seed size on seed germination, seedling emergence and seedling biomass of *Anabasis* aphylla. Pak. J. Bot., 49(2): 391-396.
- Wang, Y., J. Wang, I. Lai, L. Jiang, P. Zhuang, L. Zhang, Y. Zheng, Y., J.M. Baskin and C.C. Baskin. 2014. Geographic variation in seed traits within and among forty-two species of Rhododendron (Ericaceae) on the Tibetan plateau: Relationships with altitude, habitat, plant height, and phylogeny. *Ecol. Evol.*, 4 (10): 1913-1923.
- Wen, Y., M. Tang, D. Sun, H. Zhu, J. Wei, F. Chen and L. Tang. 2014. Influence of climatic factors and soil types on seed weight and oil content of *Jatropha Curcas* in Guangxi, China. *Proc. Environ. Sci.*, 12: 439-444.
- Westoby, M., B. Rice and J. Howell. 1990. Seed size and plant growth form as factors in dispersal spectra. *Ecology*, 71: 1307-1315.
- Wolfe, L.M. 1995. The genetics and ecology of seed size variation in a biennial plant, *Hydrophyllum appendiculatum* (Hydrophyllaceae). *Oecologia*, 101: 343-325.
- Wright, I.J. and M. Westoby. 1999. Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. J. Ecol., 87: 85-97.

(Received for publication 27 January 2017)