Pak.J.Bot., 31(2): 253-263, 1999.

SEED SIZE VARIATION AND ITS EFFECTS ON GERMINATION, GROWTH AND SEEDLING SURVIVAL IN *ACACIA NILOTICA* SUBSP. *INDICA* (BENTH.) BRENAN

S. SHAHID SHAUKAT, ZAMIN S. SIDDIQUI AND SEEMI AZIZ

Department of Botany,
University of Karachi, Karachi-75270, Pakistan

Abstract

The importance of seed size in germination, emergence, growth and survivorship was assessed. Seed weight of *Acacia nilotica* subsp. *indica* varied from 0.1104 to 0.2490 g per seed with a coefficient of variation of 19.56%. Larger seeds showed greater rate and final germination percentage compared to medium and small size seeds. Survivorship curves for all three seed size categories approached Deevy type II curves but the curves for medium and small-sized seeds were slightly steeper. Final surviving percentage of seedlings after 120 days was higher for large seeds compared to that of medium and small seeds. Seedling fresh and dry weights after 120 days of growth were greater for the ones developed from large seeds. It is concluded that variation in seed size produces variation in seedling fitness.

Introduction

Seed size, dispersal and dormancy are three related seed characteristics that are regarded as ecologically important life-history traits and reduce the risk in variable environments (Gross & Kromer, 1986; Venable & Brown, 1988; Stamp, 1990). The individual seed size (mass) in a species varies from nearly constant (Harper *et al.*, 1970; Fenner, 1985) to as high as 16-fold (Mazer, 1987; Hawke & Maun, 1989; Thompson & Pellmyr, 1989). Several factors such as competition among individual seeds for limited resources (Stanton, 1984a; Wulff, 1986), time of ovule fertilization (Cavers & Steel, 1984; McGinley, 1989; Thomson & Pellmyr, 1989), position of an ovule within the seed parent (Gray & Thomas, 1982; McGinley *et al.*, 1987; Winn, 1991), differences in habitat/microhabitat (Salisbury, 1974; Keddy, 1982; Mazer, 1989), genetic control (Stanton, 1984a; Krannitz *et al.*, 1991), and tradeoff between seed size and seed number (Werner & Platt, 1976) may be responsible for this variation.

Seed size variation has been shown to have several important ecological implications. It may affect seed germination (Weis, 1982; Alexander & Wolff, 1985; Aiken & Springer, 1995), emergence (Finstad, 1984; Berdahl & Barker, 1985; Zhang & Maun, 1990), seedling establishment (Schall, 1980; Gross & Werner, 1982; Winn, 1985), growth rate (Marshall, 1986; Zhang & Maun, 1990), plant size (Parrish & Bazzaz, 1985; Wulff, 1986), survivorship (Carleton & Cooper, 1972; Marshall, 1986; Bonfil, 1998), competitive ability (Dolan, 1984; Stanton, 1984), and reproductive ability of adult plants (Stanton, 1984). Large seeds tend to produce seedlings that are more likely to survive to maturity than seedlings from smaller seeds, though not always (Carleton & Cooper, 1972; Marshall, 1986; Wulff, 1986b; Bonfil, 1998).

An important effect of variation in seed size may be its influence on the kind of microsite in which germination and seedling establishment is possible (Janzen, 1977; Gross & Werner, 1982; Gross, 1984). Thus seed mass variation plays an important role in establishment and persistence of a species in variable or patchy environment.

Acacia nilotica subsp. *indica* (Benth.) Brenan (Fabaceae) is a multipurpose tree distributed throughout dry hot regions of India and in Sindh and Punjab provinces of Pakistan (Toky & Bisht, 1992). The objectives of this study were: (1) to determine the seed size variation pattern in a population of *A. nilotica* subsp. *indica*, (2) to evaluate the effect of seed size on germination and emergence, (3) to examine the relation between seed size and seedling survival and performance.

Materials and Methods

Seed collection and storage: Mature fruits of *Acacia nilotica* subsp. *indica* were harvested in June, 1996 near Gharo, 35 km east of Karachi city. Fruits were randomly collected from 10 different plants of the same population. Seeds were extracted from fruits, separated from pulp, washed and air-dried at room temperature overnight. Seeds with any sign of insect infestation were discarded. Clean seeds were then stored in a cool incubator at 10°C for about 2 months.

Seed weight: From a sample of about 1000 seeds a subsample of 200 seeds was randomly drawn. Seeds were then individually weighed. The frequency distribution of seed size was constructed and mean, dispersion statistics were calculated and symmetry, skewness and kurtosis were tested (Sokal & Rohlf, 1995). Seeds were sorted into three nonoverlapping size classes containing seeds weighing 0.11-0.15, 0.16-0.20 and 0.21-0.25 g categorized as small, medium and large, respectively.

Germination test: Seeds were mechanically scarified using sand paper # 3. Ten seeds with 5 replications from each size class were placed in 10 ml of distilled water in 9.5 cm diameter Petri plates with two layers of Whatman No. 1 filter paper. The Petri plates were kept randomly in a growth chamber maintained at alternating temperature with 14h illumination (36 μmol m^{-2} S^{-1}, cool white fluorescent tubes) at 30°C and 10h darkness at 25°C. Preliminary observations showed that seeds of *A. nilotica* subsp. *indica* germinated well under these environmental conditions. Germination of seeds in each size class was monitored daily for 18 days. Seeds were considered to be germinated when the protruding radicle reached a length of 2 mm (Teketay, 1995). At the termination of the 18- day germination period, root and shoot lengths of the seedlings were measured. Germination velocity (GV) was calculated using the index proposed by Mugnisjah & Nakamura (1986).

Seedling survival: For each of the three size categories ten mechanically scarified seeds were sown in each of ten 40 cm diameter earthen pots containing sandy loam soil (sand 77.2%, silt 10.2%, clay 12.6%). Seeds were sown at a depth of 1.5 cm. After one week when emergence had occurred, seedlings were thinned to six seedlings per pot. The experiment was performed in a randomized complete block design. Seedling survival was recorded at 15 days interval for 120 days. At the termination of the experiment root and shoot length and fresh and dry weights of seedlings were determined.

Statistical analysis: Percentage germination data were transformed by an arcsin square root values before subjecting the data to factorial analysis of variance (FANOVA) (Sokal & Rohlf, 1995). For the seedling survival data, a life-table was calculated for each size category (Silvertown, 1987). A Mantel-Haenszel chi-square test was performed to compare the survival rates between size categories (Deshpande *et al.*, 1995).

Results

Seed size variation: The seed weight of *Acacia nilotica* subsp. *indica* varied from 0.1104 to 0.2490 g (range=0.1386 g) and the mean seed weight of the population was 0.1774 $\pm$ 0.0024 g (mean $\pm$ standard error) (Fig. 1). Coefficient of variation was low 19.56%. The standadized value of Wilcoxon signed rank statistic (W^{++}) was 1.5105 (p=0.131) showing no significant departure from symmetry about the median value of 0.1726. Coefficient of skewness (τ_1) was 0.1919 which was non-significant and coefficient of kurtosis (τ_2) was 2.145 indicating slightly platykurtic distribution.
Germination: In all three size categories, germination started on the third day and was essentially completed by the thirteenth day (Fig. 2). Germination velocities (GV) for large, medium and small seeds were 12.45, 11.02 and 11.03, respectively thereby showing slightly greater germination velocity for larger seeds than medium and small ones. Germination was initiated earlier (at 2 days of imbibition) in larger than in medium and small sized seeds where it was initiated 3 days after imbibition.

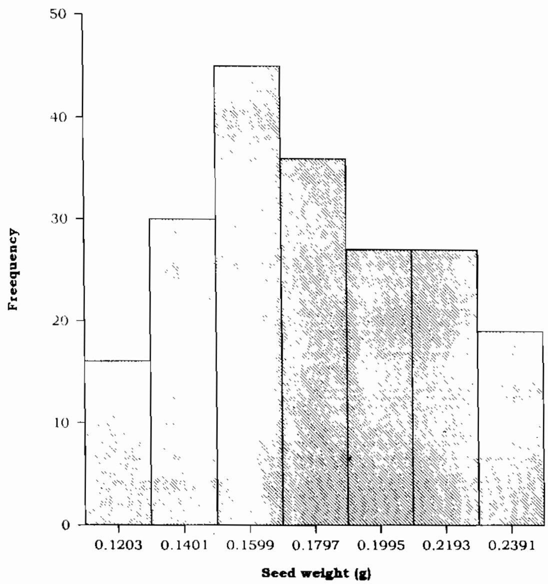

Fig.1. The frequency distribution of the seed weight of *Acacia nilotica* subsp. *indica* population at Gharo, southern Sind, Pakistan.

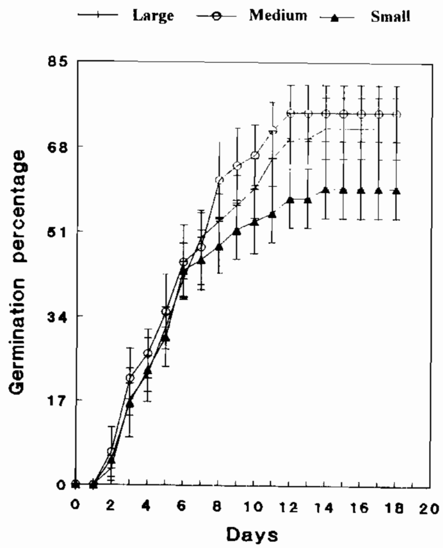

Fig.2. Cumulative germination percentage over time of *Acacia nilotica* subsp. *indica* seeds belonging to three size categories.

The results of FANOVA showed significant effect of seed size on germination percentage ($F=5.8$, $p<0.01$). Effect of time was highly significant ($F=60.27$, $p<0.001$). However, the interaction of seed size and time was non-significant ($F=0.49$ n.s.). The final germination percentage was significantly greater ($p<0.05$ and $p<0.01$) in large and medium sized seeds compared to small seeds. Both shoot and root lengths of the seedlings obtained from large seeds were significantly greater than those of small or medium sized seeds ($p<0.05$). Similarly, root/shoot ratio was significantly higher for seedlings from large seeds than for those from small and medium seeds ($p<0.05$) (Table 1).

Table 1. Root and shoot lengths and root/shoot (R/S) ratios of the 18-day old seedlings of *Acacia nilotica* developed from seeds of three different sizes.

Seed size	Root length (cm)	Shoot length (cm)	R/S ratio
Large	5.4±0.34	3.41±0.30	1.58
Medium	3.9±0.28	2.75±0.22	1.42
Small	3.6±0.36	2.45±0.34	1.47

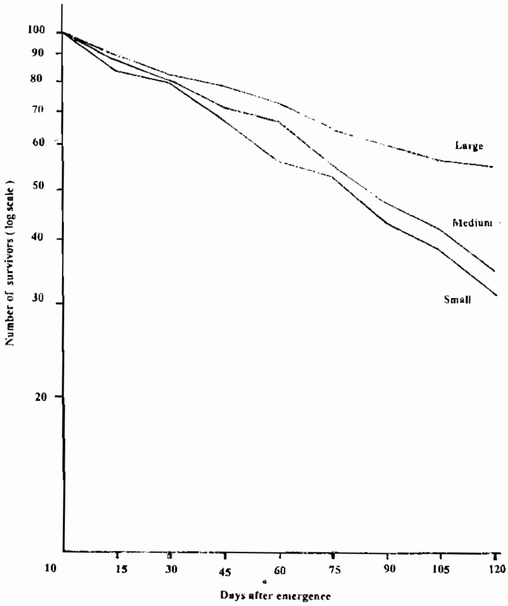

Fig.3. Survivorship curves of the seedling of *A. nilotica* subsp. *indica* raised from seeds of three different size categories.

Seedling survival: Survivorship curves of seedlings from large, medium and small seeds were close to a Deevy type II curve (Fig. 3) with more or less constant age specific mortality (Table 2). However, survivorship curves for medium and small seeds were steeper than that for large seeds. In both these data sets, the age-specific mortality increased substantially at the last observation period (Table 2). The comparison of survivorship curves using Mentel-Haenszel chi-square test showed no significant difference between curves for seedlings from small and medium seeds (X^2=2.828, n.s.), a significant difference between curves for seedlings from small and large seeds (X^2=21.624, $p<0.01$), but no significant difference between curves for seedlings from medium and large seeds (X^2=11.391, n.s.).

Table 3. Root length, shoot length and fresh and dry weights of 120 day-old seedlings of Acacia nilotica developed from seeds of three different size categories.

Seed size	Shoot length (cm)	Root length (cm)	Fresh weight (g)	Dry weight (g)
Small	30.92±1.37	13.28±1.29	19.89±0.52	4.89±0.24
Medium	44.28±1.49	22.17±0.98	27.64±0.84	6.53(0.20
Large	54.94±1.51	28.94±1.21	35.37±2.37	9.28±0.94

Shoot and root lengths differed significantly among the seedlings developed from seeds of the different size categories ($F=90.2$, $p<0.001$ and $F=52.25$, $p<0.001$ respectively). Likewise, fresh and dry weights of the seedlings obtained from the three seed size categories differed significantly ($F=59.55$, $p<0.001$ and $F=22.12$, $p<0.001$ respectively) (Table 3).

Table 2. Life tables of *Acacia nilotica* seedlings experimentally grown using seeds of three different size (weight) categories.

Seed size	Age (days)	Observed number	Number surviving out of 100	Number dying (d_x)	Age specific mortality (q_x)	Average expectancy of further life (e_x)
	0	60	10	17	0.170	68.70
	15	50	83	6	0.072	71.10
	30	46	77	9	0.116	61.05
	45	41	68	11	0.161	53.10
Small	60	34	57	4	0.070	46.95
	75	32	53	10	0.188	34.95
	90	26	43	5	0 116	26.32
	105	23	38	6	0.157	13.85
	120	19	32	-	-	-
	0	66	10	13	0.130	77.55
	15	52	87	7	0.080	73.09
	30	48	80	8	0.100	63.84
	45	43	72	5	0.069	61.62
Medium	60	40	67	12	0.179	51.13
	75	33	55	8	0.145	40.84
	90	28	47	5	0.106	28.62
	105	25	42	7	0.166	14.73
	120	21	35	-	-	-
	0	60	100	10	0.100	87.22
	15	54	90	8	0.088	81.08
	30	49	82	4	0.048	73.26
	45	47	78	6	0.076	61.63
Large	60	43	72	7	0.097	51.13
	75	39	65	5	0.076	40.84
	90	36	60	3	0.050	28.62
	105	34	57	2	0.035	14.73
	120	33	55	-	-	-

Discussion

The higher final germination percentage in large than in medium and small seeds of *Acacia nilotica* subsp. *indica*(Fig. 2) is similar to previous reports for other plant species, including *Lupinus texensis, Plantago lanceolata, Sesbania* spp., *Andropogon gerardii*, (Schaal, 1980; Weis, 1982; Alexander & Wulff, 1985; Marshall, 1986; Springer, 1991; Aiken & Springer, 1995). However, germination percentages were not affected by seed size in *Agropyron psammophilum*, and a number of wetland species (Zhang & Maun, 1990; Shipley & Parent, 1999). Decreased seed weight can be disadvantageous, since small seeds, as discussed above, is often associated with lower germination percentage and smaller seedlings that would decrease the chances of seedling establishment and survival to reproduction (Stanton, 1984; Krannitz *et al.*, 1991).

The increased germination velocity for large seeds of *A. nilotica* corroborates the findings for Sharma *et al.*, (1978), Marshall (1986) and Zhang & Maun (1990). By contrast, Stamp (1990) found a decreased rate of germination for large seeds in *Erodium brachycarpum* and Cooper *et al.*, (1979) recorded decreased germination rate with increasing seed size in *Medicago sativa*. Interestingly, Hendrix (1984) found increase or decrease in germination rate with the increase in seed size depending on conditions. The root and shoot lengths of 18-day-old seedlings were found to be greater for larger seeds compared to those developed from medium and small seeds. Similarly, Mian & Nafziger (1994) reported a direct relationship between seed size of *Triticum aestivum* L. and seedling shoot and root weight. Seedling root and shoot length for big bluestem (*Andropogon gerardii*) correlated with caryopsis size (Springer, 1991).

Increased emergence from the soil with increasing seed size observed here has also been previously reported (Bhat, 1973; Berdah & Barker, 1984; Finstad, 1984; Carren *et al.*, 1987; Zhang & Maun, 1990).

Seed size had a clear effect on survival of *A. nilotica*, with seedlings from large seeds having the highest and those from small seeds the lowest survival. Marshall (1986) studied the relationship between seed size and survival and to some extent controlled for genetic versus environmental effects by comparing the effect of seed size differences within and among three species of *Sesbania*. Largest-seeded species (*S. vesicaria*) produced seedlings that survived the longest while the smallest-seeded species (*S. macrocarpa*) produced seedlings that were relatively short-lived. However, within species effects of seed size were not clear. On the other hand Schall (1980) found larger seeds/seedlings to have higher survivorship in *Lupinus texensis*. Likewise, Krannitz *et al.*, (1991) demonstrated that seedlings of genotypes of *Arabidopsis thaliana* with larger seeds survive longer than seedlings of genotypes with smaller seeds. Bonfil (1998) working with two species of *Quercus* found a clear effect of seed size on seedling survival with large seeds having the highest and seedlings from small seeds the lowest survival.

The increased shoot and root length as well as fresh and dry weight of seedlings with an increase in size of *A. nilotica* seeds (Table 3) has also been reported for other tree species (Foster & Jonson, 1985; Tripathi & Khan, 1990; Tecklin & McCreary, 1991; Bonfil, 1998). It is generally agreed that large seeds produce larger seedlings than small ones (Harper & Obeid, 1967; Schaal, 1980; Zimmerman & Weis, 1983; Zhang & Maun, 1990). Regarding subsequent seedling growth, two patterns have been observed: (1) a consistently greater growth rate of seedlings derived from large seeds than of those from small seeds is maintained (Schaal, 1980; Stanton, 1984) and (2) the initial increase in size of seedlings produced by large seeds vanishes later because of higher growth rate of seedlings from small seeds (Lewis & Garcia, 1979; Zimmerman & Weis, 1983). The seedlings of *Acacia nilotica* seem to follow the first pattern as after 120 days of growth the size advantage of the seedlings derived from large seeds was maintained.

The significance of seed weight variation in a species depends on both the timing and magnitude of any seed weight effects on seedling growth and survival in the field. Individuals from large seeds may gain advantage early in life, particularly when seed weight affects seedling size and competitive ability (Howell, 1981; Howe & Richter, 1982; Gross, 1984), resistance to moisture stress (Baker, 1972; Weis, 1982; Armstrong & Westoby, 1993) or tolerance to shade (Leishman & Westoby, 1994; Saverimuttu & Westoby, 1996).

Given the large intrapopulation variation in seed size, other ecological factors, such as dispersal, seedling establishment, seed predation and water relations may confer an advantage to different seed sizes (Stanton, 1985; Kelly & Purvis, 1993). Requirements of safe-site would also differ for seeds of different sizes. Safe-site requirements of small seeds are more restrictive than those of large seeds (Winn, 1985). Thus, variation in seed size has great ecological significance in the establishment and maintenance of populations, particularly in harsh and variable environments, which in turn plays a significant role in the evolutionary success of a species.

References

Aiken, G.E. and T.L. Springer. 1995. Seed size distribution, germination and emergence of 6 switchgrass cultivars. *J. Range Manage.*, 48: 455-458.

Alexander, H.M. and R.D. Wulff. 1985. Experimental ecological genetics in *Plantago*. X. The effects of maternal temperature on seed and seedling characters in *P. lanceolata*. *J. Ecol.*, 73: 271-282.

Armstrong, D.P. and M. Westoby. 1993. Seedlings from large seeds tolerate defoliation better: a test using phytogenetically independent contrasts. *Ecology*, 74: 1092-1100.

Baker, H.G. 1972. Seed weight in relation to environmental conditions in California. *Ecology*, 53: 997-1010.

Berdahl, J.D. and R.E. Barker. 1984. Selection for improved seedling vigor in Russian wild ryegrass. *Can. J. Bot.*, 64: 131-138.

Bhat, J.L. 1973. Ecological significance of seed size to emergence and dormancy characteristics in *Indigofera glandulosa*. *Jap. J. Ecol.*, 23: 95-99.

Carleton, A.E. and C.S. Cooper. 1972. Seed size effects upon seedling vigor of three forage legumes. *Crop Sci.*, 12: 183-186.

Carren, C.J., A.M. Wilson, R.L. Cuany and G.L. Thor. 1987. Caryopsis weight and planting depth of blue grama. I. Morphology, emergence and seedling growth. *J. Range Manage.*, 40: 207-211.

Cavers, P.B. and M.G. Steel. 1984. Patterns of change in seed weights over time on individual plants. *Amer. Nat.*, 124: 324-335.

Cooper, C.S., R.L. Ditterline and L.E. Welty. 1979. Seed size and seedling rate effects upon stand density and field of alfalfa. *Agron. J.*, 71: 83-85.

Deshpande, J.V., A.P. Gore and S. Shanubhogue. 1995. *Statistical analysis of nonnormal data*. Wiley Eastern, Delhi.

Dolan, R.W. 1984. The effect of seed size and maternal source on individual size in a population of *Ludwigia leptocarpa* (Onagraceae). *Amer. J. Bot.*, 71: 1302-1307.

Fenner, M. 1985. *Seed ecology*. Chapman and Hall, New York.

Finstad, K. 1984. *Emergence, seedling growth and water relations of grasses on sandy substrates*. M.Sc. thesis, University of Saskatchewan, Saskatoon, Canada.

Foster, S.A. and C.H. Janson. 1985. The relationship between seed size and establishment conditions in tropical woody plants. *Ecology*, 66: 773-780.

Gray, D. and T.H. Thomas. 1982. Seed germination and seedling emergence as influenced by the position and development of the seed on and chemical applications to the parent plant. In: *The physiology and biochemistry of seed development, dormancy and germination*, (Ed.) A.A. Khan. 81-110. Elsevier Biomedical Press, New York.

Gross, K.L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennials. *J. Ecol.*, 72: 369-387.

Gross, K.L. and M.L. Kromer. 1986. Seed weight effects on growth and reproduction in *Oenothera biennis* L. *Bull. Torrey Bot. Club*, 113: 252-258.

Gross, K.L. and P.A. Werner. 1982. Colonizing abilities of "biennial" plant species in relation to ground cover: Implications for their distribution in a successional sere. *Ecology*, 63: 921-931.

Harper, J.L., P.H. Lovell and K.G. Moore. 1970. The shapes and sizes of seeds. *A. Rev. Ecol. Syst.*, 1: 327-356.

Harper, J.L. and M. Obeid. 1967. Influence of seed size and depth of sowing on the establishment and growth of varieties of fiber and oil seed flax. *Crop Sci.*, 7: 527-532.

Hawke, M.A. and M.A. Maun. 1988. Some aspects of nitrogen, phosphorus, and potassium nutrition of three colonizing beach species. *Can. J. Bot.*, 6: 1490-1496.

Hendrix, S.D. 1984. Variation in seed weight and its effects on germination of *Pastinaca sativa* (Umbelliferae). *Amer. J. Bot.*, 71: 795-802.

Howe, H.F. and W.M. Richter. 1982. Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Oecologia*, 53: 347-351.

Howell, N. 1981. The effect of seed size and relative emergence time on fitness in a natural population of *Impatiens capensis* Meerb. (Balsaminaceae). *Am. Midl. Nat.*, 105: 312-320.

Janzen, D.H. 1977. Variation in seed size within a crop of Costa Rican *Mucuna andreana* (Leguminosae). *Amer. J. Bot.*, 64: 347-349.

Keddy, P.A. 1982. Population ecology on an environmental gradient: *Cakile edentula* on a sand dune. *Oecologia*, 52: 348-355.

Kelly, C.K. and A. Purvis. 1993. Seed size and establishment conditions in tropical trees. *Oecologia*, 94: 356-360.

Krannitz, P.G., L.W. Aarssen and J.M. Dow. 1991. The effect of genetically based differences in seed size on seedling survival in *Arabidopsis thaliana* (Brassiceae). *Amer. J. Bot.*, 78: 446-450.

Leishman, M.R. and m. Westoby. 1994. The role of large seed size in shaded conditions: experimental evidence. *Functional Ecol.*, 8: 205-214.

Lewis, E.J. and J.A. Garcia. 1979. The effect of seed weight and coleoptile tiller development on seed vigour in tall fescue *Festuca arundinacea* Screb. *Euphytica*, 28: 393-402.

Marshall, D.L. 1986. Effect of seed size on seedling success in three species of *Sesbania* (Fabaceae). *Amer. J. Bot.*, 73: 457-464.

Mazer, S.J. 1987. The quantitative genetics of life history and fitness components in *Raphanus raphanistrum* L. (Brassicaceae): ecological and evolutionary consequences of seed size variation. *Am. Nat.*, 130: 891-914.

Mazer, S.J. 1989. Ecological, taxonomic and life history correlates of seed mass among Indiana dune angiosperms. *Ecol. Monogr.*, 59: 153-175.

McGinley, M.A. 1989. Within and among plant variation in seed mass and pappus size in *Tragopogon dubius*. *Can. J. Bot.*, 67: 1298-1304.

McGinley, M.A., D.H. Temme and M.A. Geber. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *Am. Nat.*, 130: 370-398.

Mian, M.A.R. and E.D. Nafziger. 1994. Seed size and water potential effects on germination and seedling growth of winter wheat. *Crop Sci.*, 34: 169-171.

Mugnisjah, W.Q. and S. Nakamura. 1986. Stress for seed vigour evaluation in soybean. *Seed Sci. Technol.*, 14: 95-103.

Parrish, J.A.D. and F.A. Bazzaz. 1985. Nutrient content of *Abutilon theophrasti* seeds and the competitive ability of resulting plants. *Oecologia*, 65: 247-251.

Salisbury, E.J. 1974. *Seed size and mass in relation to environment. Proc. Royal Soc. London*, B186: 83-88.

Saverimuttu, T. and M. Westoby. 1996. Seedling longevity under deep shade in relation to seed size. *J. Ecol.*, 84: 681 689.

Schail, B.A. 1980. Reproductive capacity and seed size in *Lupinus texensis*. *Amer. J. Bot.*, 67: 703-709.

Sharma, M.M., N.K. Sharma and D.N. Sen. 1978. A new report on differential seed coat dormancy in *Sesbania bispinosa* (Jacq.) W.F. *Right Folia Geobot. Phytotax.*, 13: 95-98

Shipley, B. and M. Parent. 1991. Germination responses of 64 wetland species in relation to seed size, minimum time to reproduction and seedling relative growth rate. *Funct. Ecol.*, 5: 111-118.

Silvertown, J.W. 1987. *Introduction to plant population ecology*. Longman, Harlow, Essex.

Sokal, R.R. and E.J. Rholf. 1995. *Biometry*, 3rd ed. Freeman, San Francisco, CA.

Springer, T.L. 1991. Caryopsis size and germination of *Andropogon gerardii* pedicellate and sessile spikelets. *Seed Sci. Technol.*, 19: 461-468.

Stamp, N.E. 1990. Production and effect of seed size in a grassland annual (*Erodium brachycarpum*, Geraniaceae). *Amer. J. Bot.*, 77: 874-882.

Stanton, M.L. 1984a. Developmental and genetic sources of seed weight variation in *Raphanus raphanistrum* L. (Brassicaceae). *Amer. J. Bot.*, 71: 1090-1098

Stanton, M.L. 1984b. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology*, 65: 1105-1112

Stanton, M. 1985. Seed size and emergence time within a stand of wild radish (*Raphanus raphanistrum* L.): the establishment of a fitness hierarchy. *Oecologia*, 67: 524-531.

Tecklin, J. and D.D. McCreary. 1991. Acorn size as a factor in early seedling growth of blue oak. *USDA Forest Service General Technical Report PSW*, 126: 48-53.

Teketay, D. 1996. Germination ecology of twelve indigenous and eight exotic multipurpose leguminous species from Ethiopia. *For. Ecol. Manage.*, 80: 209-223.

Thompson, J.N. and O. Pellmyr. 1989. Origins of variance in seed number and mass: interaction of sex expression and herbivory in *Lomatium salmoniflorum*. *Oecologia*, 79: 395-402.

Toky, O.P. and R.P. Bisht. 1992. Observations on the rooting patterns of some agroforestry trees in an arid region of north-western India. *Agrofor. Syst.*, 18: 245-263.

Tripathi, R.S. and M.L. Khan. 1990. Effect of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet forest. *Oikos*, 57: 289-296.

Venable, D.L. and J.S. Brown. 1988. The selective interactions of dispersal, dormancy and seed size as adaptations for reducing risk in variable environments. *Am. Nat.*, 131: 360-384.

Weis, Y.M. 1982. The effect of propagule size on germination and seedling growth in *Mirabilis hirsuta*. *Can. J. Bot.*, 60: 1868-1874.

Werner, P.A. and W.J. Platt. 1976. Ecological relationships of co-occurring golden rods (Solidago: Compositae). *Am. Nat.*, 110: 959-971.

Winn, A.A. 1985. The effect of seed size and microsite on seedling emergence in four field populations of *Prunella vulgaris*. *J. Ecol.*, 73: 831-840.

Winn, A.A. 1991. Proximal and ultimate sources of within-individual variation in seed mass in *Prunella vulgaris* (Lamiaceae). *Amer. J. Bot.*, 78: 838-844.

Wulf, R.D. 1986a. Seed size variation in ***Desmodium paniculatum***. I. Factors affecting seed size. *J. Ecol.*, 74: 87-97.

Wulf, R.D. 1986b. Seed size variation in *Desmodium paniculatum*. II Effect on seedling growth and physiological performance. *J. Ecol.*, 74: 99-14.

Zhang, J. and M.A. Maun. 1990. Seed size variation and its effects on seedling growth in *Agropyron psammophilum*. *Bot. Gaz.*, 151: 106-113.

Zimmerman, J.K. and J.M. Weis. 1983. Fruit size variation and its effect on germination and seedling growth in *Xanthium strumarium* L. *Can. J. Bot.*, 61: 2309-2315.

(Received for publication 23 September 1999)