



Characterizing plant attributes with particular emphasis on seeds in Tamaulipan thornscrub in semi-arid Mexico

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Seed mass, dispersal syndromes and other plant attributes were investigated for 111 species native to north-eastern Mexico. We investigated whether seeds from Mexico conformed to patterns of seed size and dispersal syndrome spectra found for floras in arid environments from around the world. The distribution of seed mass in the Mexican flora (0.03–598 mg) was generally similar to that found elsewhere. All of the major seed dispersal syndromes previously found in arid environments were represented in Mexico, although vertebrate dispersal (33 species) was unusually common. There were 31 species having wind-dispersed seeds, four ant-dispersed and 43 with no obvious dispersal morphology. Woody species were more likely to have large seeds and herbaceous species were more likely to have small seeds. Woody plants had proportionally more wind-dispersed and less animal-dispersed species than did herbaceous plants. We did not find the expected relationship between time of seed set of vertebrate-dispersed species and the presence of migratory birds or between time of seed set and optimum germination time.

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Introduction

Plants produce seeds (i.e. the sexual reproductive unit, be it seeds, fruits or fruits with accessories) in a broad range of shapes and sizes (Harper *et al.*, 1970). Within any given habitat, seed size usually varies over five or six orders of magnitude (Baker, 1972; Foster & Janson, 1985; Mazer, 1989; Jurado *et al.*, 1991; Westoby *et al.*, 1992; Leishman *et al.*, 2000). Seeds also display a wide range of dispersal structures, including fleshy fruits, lipid-rich elaiosomes, and elaborate wings or plumes. This wide variation in seed morphology is ecologically significant in many ways.

Seedlings from larger seeds have been shown experimentally to have greater tolerance of a variety of stresses, including clipping (Armstrong & Westoby, 1993), deep shade

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(Saverimuttu & Westoby, 1996) and nutrient deprivation (Jurado & Westoby, 1992). Seedlings from large-seeded species also have a competitive advantage over seedlings from small-seeded species (Turnbull *et al.*, 1999; Leishman *et al.*, 2000). However, the apparent advantages of producing large seeds are balanced by the seed size/number tradeoff. That is, a plant with a given amount of resources available for reproduction can produce many small seeds, or fewer larger seeds (Smith & Fretwell, 1974; Haig & Westoby, 1990; Jakobsson & Eriksson, 2000).

Seed size is correlated with many other important plant traits, including relative growth rate, growth form, height and dispersal syndrome. Large-seeded species generally have lower relative growth rates than do small-seeded species (Marañón & Grubb, 1993; Jurado & Westoby, 1992). This is important in situations where speed of establishment is critical, such as recently disturbed sites. Woody and taller species tend to produce larger seeds (Salisbury, 1942; Baker, 1972; Foster & Janson, 1985; Michaels *et al.*, 1988; Mazer, 1989; Jurado *et al.*, 1991; Leishman & Westoby, 1994; Hammond & Brown, 1995; Leishman *et al.*, 1995; Lord *et al.*, 1995; Metcalfe & Grubb, 1995). Small-seeded species are more likely to have unassisted seed dispersal, and larger seeded species are more likely to be animal dispersed (Jurado *et al.*, 1991; Hughes *et al.*, 1994; Leishman *et al.*, 1995).

Seed dispersal is the means by which plants find new sites for establishing seedlings, it is expected that dispersal should be directed to safe sites where seeds are more likely to establish a seedling (Harper, 1977). For some arid environments, it has been proposed that safe sites are so rare that it is more efficient to avoid dispersal and use the mother's site when it becomes available (Ellner & Schmid, 1981). Selection of dispersal syndromes is likely to differ according to environments (Oakwood *et al.*, 1993). For instance elaiosomes (food bodies that are found to be associated with ant dispersal) are very common in ant rich ecosystems (Hughes *et al.*, 1994). The presence of adhesive diaspores is more common where chances of mammals moving the seeds are high (e.g. grasslands) (Jurado *et al.*, 1991; Morton & Baynes, 1985). Fleshy fruits are common where birds and arboreal mammals are numerous such as in rainforests (Foster & Janson, 1985). Wind adapted diaspores are expected to be more frequent in environments where wind is an important factor (Jurado *et al.*, 1997; Gentry, 1982) such as arid open environments like the Indian desert where wind-dispersal is the most common syndrome (Bansal & Sen, 1981).

Seed dispersal syndromes have been found to be associated with other plant traits such as seed size, for instance very heavy seeds have been arguably associated as a means to prevent dispersal in some arid environments (Ellner & Schmid, 1981). Very small seeds are expected to be associated with wind dispersal by virtue of their size (< 0.1 mg), and hence have no additional structures to enhance wind dispersal (Leishman & Westoby, 1994). Adhesive diaspores are expected to be light (Sorensen, 1986), so that they are not immediately noticed and discarded by dispersal agents at a very short dispersal distance.

No previous studies have quantified seed attributes for large numbers of species from Mexico. In this paper, we investigated whether seed biology of Tamaulipan thornscrub (matorral) conforms to the patterns of seed size and dispersal syndromes spectra found for other floras around the world. We also used our data to answer questions regarding seed mass, climate and plant life form, and investigated potential relationships between dispersal and season of seed production, dispersal and seed mass and plant life form.

Methods

This study was conducted in Tamaulipan thornscrub near Linares, Nuevo Leon, Mexico (24°47'N; 99°32'W; 360 m a.s.l.). Linares has a mean annual rainfall of 810.6 mm, which falls mainly in late spring and early autumn (Cavazos & Molina,

1992). Mean annual temperature is 22.4°C, with 41.1°C and –2.3°C being the mean maximum and mean minimum daily temperatures (Cavazos & Molina, 1992). The highest temperatures and the lowest precipitation both occur in July and August (Cavazos & Hastenrath, 1990).

Tamaulipan thornscrub includes up to 60 shrub and tree species with an average height of 4 m, half of which are thorny (Reid *et al.*, 1990; Jurado *et al.*, 1998). Thornscrub is native to Linares, but is thought to have increased in extent due to fire suppression and grazing practices in the past centuries (Archer, 1995; Brown & Archer, 1999).

Data on seed mass, dispersal syndrome, and plant attributes were gathered for 111 species (as many species as we could find seeds for). At least 50 seeds were collected from more than 20 mature plants for each species. Seed mass was measured for at least 20 individual seeds per species. Seed coat (but not dispersal structures) was included in seed mass following Jurado *et al.* (1991) and Westoby (1998). Seeds were dried at 80°C until constant weight. Dispersal syndromes were determined with evidence of structures in the diaspores, such as flesh, elaiosomes, or wings (following Jurado *et al.*, 1991). Chi-square analyses were run for evidence of association between some seed traits and other plant attributes. Date of seed production was determined using dates of seed collection and included in season categories. For contingency tables seed mass was categorized into small (<1 mg), medium (1–9.9 mg) and large (>9.9 mg).

Results and discussion

Seed mass

Seed weight ranged from 0.03 mg (*Nicotiana glauca*) to 598 mg (*Ebenopsis ebano*) (Appendix 1). The range of seed sizes was not as great in Linares as in other floras, as no extremely large or extremely small-seeded species were present (Fig. 1). Species from the Tamaulipan thornscrub showed a log-normal distribution of seed mass, similar to that previously found in many other environments from around the world (Leishman *et al.*, 2000; Fig. 1). Compared to other floras in arid environments the mode seed mass

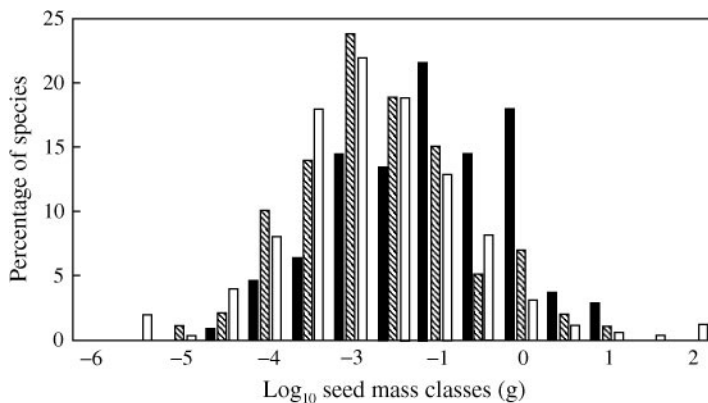


Figure 1. Frequency distribution of seed mass of seeds from California (□) (Baker, 1972), Central Australia (▨) (Jurado *et al.*, 1991) and Linares (■). There was a log-normal distribution of seed mass in the flora of Linares similar to that previously observed in other floras (Leishman *et al.*, 2000). However there were no very small or very large seeded species in Linares. The mode for Linares coincides with the mode for central Australia and these in turn are two categories heavier than the California mode.

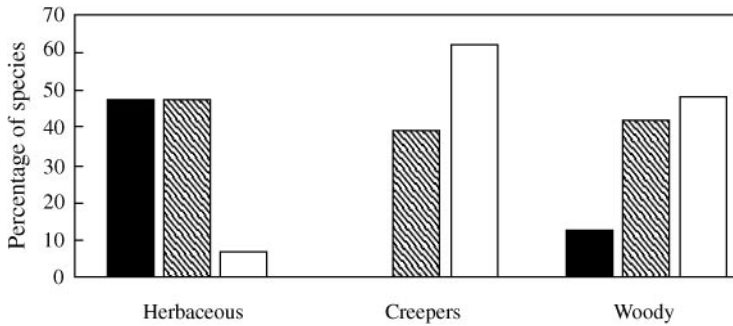


Figure 2. Life form and seed weight. Woody species (17) had more species with heavier seeds (■) and fewer with medium (▨) and small seeds (□) than expected. Whereas herbaceous species (58) had more medium and small-seeded species and less large seeded species than expected. While there was an insufficient number of creepers (13) to test for significance their trend is interesting in that they behave in the same way as woody species (Chi-square = 29.5, $df = 4$, $p < 0.0001$). Three cells had expected values less than five, however Chi square test was still significant when the creepers were excluded (Chi-square = 17.45, $df = 2$, $p = 0.0002$).

for species from Linares (6.580 mg) coincided with the mode for central Australian species (Jurado *et al.*, 1991), but was one order of magnitude heavier than the mode seed mass for Californian species (0.568 mg; Baker, 1972).

There was a relationship between plant growth form and seed mass (Fig. 2). Plants with a woody growth form were more likely to have large seeds and less likely to have small seeds than would be expected by chance. This was consistent with evidence from previous studies (Salisbury, 1942; Baker, 1972; Foster & Janson, 1985; Mazer, 1989; Jurado *et al.*, 1991; Leishman & Westoby, 1994; Hammond & Brown, 1995; Leishman *et al.*, 1995; Metcalfe & Grubb, 1995). Conversely, plants with a herbaceous growth form were more likely to have medium or small seeds and less likely to have large seeds than would be expected by chance. While there was an insufficient number of creepers to test for significance, they appeared to follow a similar pattern to woody species (Fig. 2). The low number of large-seeded herbaceous species may be underlain by the correlation between twig cross-sectional area and fruit size (Corner, 1949; Ackerly & Donoghue, 1998).

Seed mass was associated with dispersal syndromes (Fig. 3). Small-seeded species were over represented in the wind-dispersed category and under represented in the unassisted and animal-dispersed categories. Species with medium sized seeds were represented in all dispersal classes in an apparently random pattern. Large-seeded species were over-represented in the animal-dispersed category and under-represented in the wind-dispersed category. Species with vertebrate dispersal had larger seeds (Appendix 1).

These general trends are similar to those found elsewhere, including arid Australia (Jurado *et al.*, 1991), dry sclerophyl forest (Hughes *et al.*, 1994), arid, semi-arid and maritime Australian Floras (Oakwood *et al.*, 1993) and five temperate habitats around the world (Leishman *et al.*, 1995). Perhaps the cost of producing a reward for animal dispersal is high enough that it is only cost effective above a certain seed mass, when seedlings have higher chances of seedling establishment. Alternatively many 'dispersers' might easily consume a very small seed, as a hard seed coat could also be too costly for a small seed. Another potential explanation for this is that very small seeds get transported in the wind by virtue of having a high surface area to weight ratio, and an additional structure to augment wind resistance would be a cost-effective means for dispersal (Leishman & Westoby, 1994).

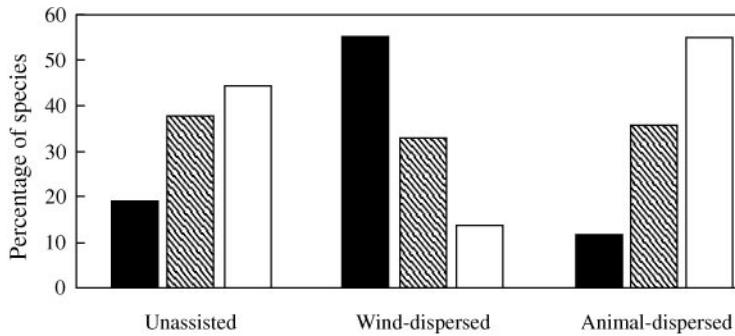


Figure 3. Dispersal syndrome and seed mass. Small-seeded species (■) were over represented in the wind-dispersed category (31 species) and under represented in the unassisted (43 species) and animal-dispersed (37 species) categories. Medium sized species (▨) values were according to random expectations while there were more large seeded species (□) associated with animal dispersal and less to wind dispersal than expected. Chi-square = 22.07, *df.* = 4, *p* = 0.0002.

Dispersal syndromes

Dispersal syndromes are presented in Appendix 1. A large group of species (37) was apparently adapted for animal dispersal. There were 31 species with diaspores that were apparently adapted for wind dispersal. Forty-three species had seeds with no obvious dispersal morphology, including six species with explosive dehiscence. Of the 37 species classed as having animal-dispersed seeds, 33 were apparently adapted for dispersal by vertebrates (of these, two species had adhesive seeds) and four for dispersal by ants.

Linares had a smaller percentage of ant, adhesive and wind dispersed species than Central Australia (Fig. 4). The fact that Linares had a higher proportion of vertebrate-dispersed seeds than Central Australia or the Negev desert in Israel (Fig. 5) could be due

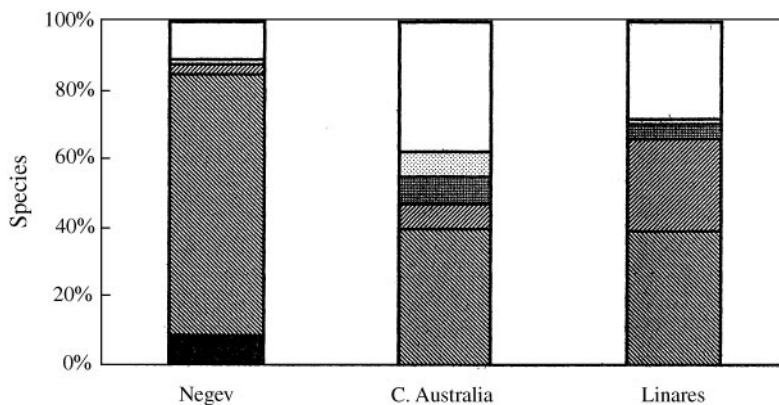


Figure 4. Dispersal syndromes in arid floras. Linares had a smaller percentage of ant (■), adhesive (▨) and wind (□) dispersed species than Central Australia (Jurado *et al.*, 1991). A tendency of vertebrate (▩) dispersal syndromes to be more common in moister environments became apparent in that a higher percentage of vertebrate dispersed species was found for Linares with lower percentages found in C. Australia and the Israeli (Negev) desert (Ellner & Schmida, 1981). Dispersal avoiders (■) were not found for Linares or Australia, while unassisted species (▧) were common in all environments.

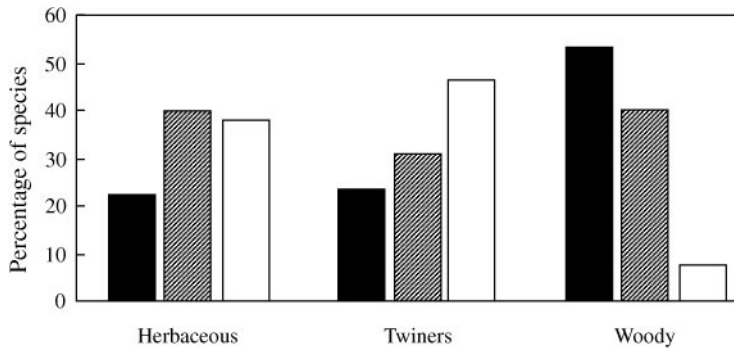


Figure 5. Life form and dispersal syndrome. Life form was associated with seed dispersal syndrome in that herbaceous species (58) were more animal-dispersed (■) and less wind-dispersed (□) than expected by chance. Woody species (40) in turn were more wind-dispersed and less animal-dispersed than expected. While there were too few creepers (13) for a significant test it is interesting that they behaved more like herbaceous than like woody species (Chi-square = 16.74, d.f. = 4, $p = 0.0022$, two cells had expected values less than 5.0). However when excluding the creepers Chi-square was still significant: Chi-square = 14.77, d.f. = 2, $p = 0.0006$. Unassisted species (□).

to the greater availability of moisture in Linares. Water limitations could make fleshy fruits expensive in dry environments. No species were considered to 'avoid' dispersal (i.e. by being produced under the soil surface) for Linares in sharp contrast with the number reported for the Negev (Ellner & Schmida, 1981). The percentage of species with unassisted seed dispersal in Linares was similar to that in the Central Australian Flora (Jurado *et al.*, 1991) and much lower than in the Negev Flora in Israel. The only two species with adhesive diaspores found here comply with Sorensen's (1986) prediction of adhesive diaspores not being too heavy as both species had seeds in the small or medium-sized categories.

There was a relationship between life form and dispersal syndrome (Fig. 5). Herbaceous species were more likely to be animal-dispersed and less likely to be wind dispersed than would be expected by chance. This is in contrast with findings for wind dispersal syndrome to be common for herbaceous species in more open environments (Grime *et al.*, 1977). Woody species in turn were more likely to be wind-dispersed and less likely to be animal-dispersed than would be expected by chance. Perhaps this is a result of woody species being more exposed to wind, and the lack of arboreal mammals in the region. While there were too few creepers for a significant test it is interesting that in terms of dispersal they behaved more like herbaceous than like woody species.

Dispersal syndrome was unrelated to season of seed collection (Fig. 6). One might have expected animal dispersed species to be produced in autumn to coincide with the presence of migratory birds (Gonzalez-Rojas, 1999). Alternatively, one might have predicted a relationship between the time of seed production and the optimal time for seedling emergence — in this case spring and autumn (Flores & Jurado, 1998; Jurado *et al.*, 1998). The lack of association suggests that there are factors other than potential dispersal by migratory birds and safe time for germination selecting for season of seed production. As seeds generally drop from the mother plant shortly after maturation, these factors might include dispersal by local birds and pollination timing (Eriksson & Ehrlén, 1998) and perhaps available resource allocation.

In conclusion, the distribution of seed masses and range of dispersal syndromes found in the Tamaulipan thornscrub flora were generally similar to those previously found in arid ecosystems elsewhere in the world. Relationships between seed mass, growth form, and dispersal mode were also similar in this flora to those elsewhere. For instance: large

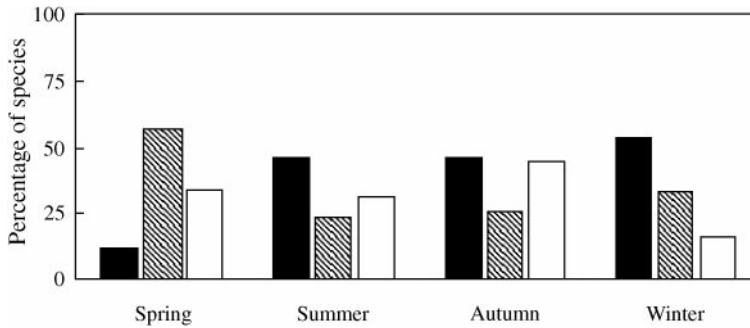


Figure 6. Dispersal syndrome and season of seed collection were not related (Chi-square = 9.40, $df = 6$, $p = 0.1525$, NB three cells had expected values less than 5.0). Unassisted species (■), wind-dispersed (▨) and animal-dispersed (□).

seeds tended to be associated with a woody growth form; small-seeds were more likely to be wind-dispersed, and large-seeds were more frequently associated with animal dispersal; herbaceous species were more likely to be vertebrate dispersed and woody species were more likely to be animal dispersed. The similarities in these broad-scale relationships suggest that some other extrapolations from studies of similar ecosystems elsewhere in the world may be applied to this little-known flora. However, there are some important factors which distinguish the flora of Linares from other arid floras, including differences in the suite of seed dispersal agents (vertebrates were relatively more important as seed-dispersers in Linares than arid environments in Australia or Israel).

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References

- Ackerley, D.D. & Donoghue, M.J. (1998). Leaf size, sapling allometry, and Corner's rules: Phylogeny and correlated evolution in maples (*Acer*). *The American Naturalist*, **152**: 767–791.
- Archer, S. (1995). Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland reconstructing the past and predicting the future. *Ecoscience*, **2**: 83–99.
- Armstrong, D.P. & Westoby, M. (1993). Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrasts. *Ecology*, **74**: 1092–1100.
- Baker, H.G. (1972). Seed weight in relation to environmental conditions in California. *Ecology*, **53**: 997–1010.
- Bansal, R.P. & Sen, D.N. (1981). Dispersal strategies in plants of the Indian Desert. *Journal of Arid Environments*, **4**: 3–14.
- Brown, J.R. & Archer, S. (1999). Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology*, **80**: 2385–2396.
- Cavazos, M.T. & Hastenrath, S. (1990). Convection and rainfall over Mexico and their modulation by the southern oscillation. *International Journal of Climatology*, **10**: 377–386.
- Cavazos, M.T. & Molina, V. (1992). Climatic records for the citrus region of Nuevo Leon. *Reporte Tecnico Facultad de Ciencias Forestales Universidad Autonoma de Nuevo Leon*, **1**: 1–65.
- Corner, E.J.H. (1949). The Durian theory or the origin of the modern tree. *Annals of Botany*, **8**: 966–952.

- Ellner, S. & Schmid, A. (1981). Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia*, **51**: 133–144.
- Eriksson, O. & Ehrlén, J. (1998). Phenological adaptations in fleshy vertebrate-dispersed fruits of temperate plants. *Oikos*, **82**: 617–621.
- Flores, J. & Jurado, E. (1998). Germination and early growth traits of 14 plant species native to northern Mexico. *The Southwestern Naturalist*, **43**: 40–46.
- Foster, S.A. & Janson, C.H. (1985). The relationship between seed size and establishment conditions in tropical woody plants. *Ecology*, **66**: 773–780.
- Gentry, A.H. (1982). Patterns in neotropical plant species diversity. *Evolutionary Biology*, **15**: 1–84.
- González-Rojas (1999). Birds of the tamaulipan thronscrub and effect of fragmentation over its diversity in ejido vistahermosa, Linares, Nuevo Leon, Mexico. Unpublished Ph.D. thesis, University of Nuevo Leon, Mexico.
- Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornellisen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodgkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Mathews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., Ross Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.A., Thorpe, P.C. & Whitehouse, J. (1977). Integrated screening validates primary axes of specialization in plants. *Oikos*, **79**: 259–281.
- Haig, D. & Westoby, M. (1990). Inclusive fitness, seed resources, and maternal care. In: Lovett Doust, L. (Ed.), *Plant reproductive ecology. Patterns and strategies*, pp. 60–79. New York: Oxford University Press. 360 pp.
- Hammond, D.S. & Brown, V.K. (1995). Seed size of woody plants in relation to disturbance, dispersal, soil type in neotropical forests. *Ecology*, **76**: 2544–2561.
- Harper, J.L. (1977). *Population biology of plants*. New York: Academic Press. 892pp.
- Harper, J.L., Lovell, P.H. & Moore, K.G. (1970). The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, **1**: 327–356.
- Hughes, L., Dunlop, M., French, K., Leishman, M.R., Rice, B., Rodgeron, L. & Westoby, M. (1994). Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. *Journal of Ecology*, **82**: 933–950.
- Jakobsson, A. & Eriksson, O. (2000). A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos*, **88**: 494–502.
- Jurado, E. & Westoby, M. (1992). Germination biology of selected central Australian plants. *Australian Journal of Ecology*, **17**: 318–330.
- Jurado, E., Westoby, M. & Nelson, D. (1991). Diaspore weight, dispersal, growth form and perenniality of Central Australian plants. *Journal of Ecology*, **80**: 417–416.
- Jurado, E., Westoby, M., Stafford-Smith, M.D. & Nelson, D. (1997). Seed and life history attributes in relation to a position in an erosion gradient in arid Australia. *Reporte Científico. Facultad de Ciencias Forestales Universidad Autónoma de Nuevo Leon*, **33**: 1–30.
- Jurado, E., Flores, J., Navar, J. & Jiménez, J. (1998). Seedling establishment under native tamaulipan thronscrub and *Leucaena leucocephala* plantation. *Forest Ecology and Management*, **105**: 151–157.
- Leishman, M.R. & Westoby, M. (1994). The role of large seed size in shaded conditions: experimental evidence. *Functional Ecology*, **8**: 205–214.
- Leishman, M.R., Westoby, M. & Jurado, E. (1995). Correlates of seed size variation: a comparison across five temperate floras. *Journal of Ecology*, **83**: 517–530.
- Leishman, M.R.W., I.J., Moles, A.T. & Westoby, M. (2000). The evolutionary ecology of seed size. In Fenner, M. (Ed.), *Seeds—the ecology of regeneration in plant communities* (2nd Edn), 31–58pp. Wallingford, UK: CAB International. 416 pp.
- Lord, J., Egan, J., Clifford, H.T., Jurado, E., Leishman, M.R., Williams, D. & Westoby, M. (1995). Larger seeds in tropical floras: consistent patterns independent of growth form and dispersal mode. *Journal of Biogeography*, **24**: 205–211.
- Marañón, T. & Grubb, P.J. (1993). Physiological basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. *Functional Ecology*, **7**: 591–599.
- Mazer, S.J. (1989). Ecological, taxonomic and life history correlates of seed mass among Indiana dune Angiosperms. *Ecological Monographs*, **59**: 153–175.
- Metcalf, D.J. & Grubb, P.J. (1995). Seed mass and light requirements for regeneration in Southeast Asian rain forest. *Canadian Journal of Botany-Revue Canadienne de Botanique*, **73**: 817–826.

- Michaels, H.J., Benner, B., Hartgerink, A.P., Lee, T.D., Rice, S., Wilson, M.F. & Bertin, R.I. (1988). Seed size variation: magnitude, distribution and ecological correlates. *Evolutionary Ecology*, **2**: 157–166.
- Morton, S.R. & Baynes, A. (1985). Small mammal assemblages in arid Australia: A reappraisal. *Australian Mammalogy*, **8**: 159–169.
- Oakwood, M., Jurado, E., Leishman, M.R. & Westoby, M. (1993). Geographic ranges of plant species in relation to dispersal morphology, growth form and diaspore weight. *Journal of Biogeography*, **20**: 563–572.
- Reid, N., Stafford Smith, D.M., Beyer-Münzel, P., Marroquín, J. (1990). Floristic and structural variation in the Tamaulipan thornscrub, northeastern Mexico. *Journal of Vegetation Science*, **1**: 529–538.
- Salisbury, E.J. (1942). *The reproductive capacity of plants*. London: G. Bell and Sons. 244 pp.
- Saverimuttu, T. & Westoby, M. (1996). Seedling longevity under deep shade in relation to seed size. *Journal of Ecology*, **84**: 681–689.
- Smith, C.C. & Fretwell, S.D. (1974). The optimal balance between size and number of offspring. *The American Naturalist*, **108**: 499–506.
- Sorensen, A.E. (1986). Seed dispersal by adhesion. *Annual Review of Ecology and Systematics*, **17**: 443–463.
- Turnbull, L.A., Rees, M. & Crawley, M.J. (1999). Seed mass and the competition/colonization trade-off: a sowing experiment. *Journal of Ecology*, **87**: 899–912.
- Westoby, M. (1998). A leaf-height-seed (LHS) plant strategy scheme. *Plant and Soil*, **199**: 213–227.
- Westoby, M., Jurado, E. & Leishman, M.R. (1992). Comparative evolutionary ecology of seed size. *Trends in Ecology and Evolution*, **7**: 368–372.

Appendix 1. Species list and attributes for Tamaulipan thornscrub in north-eastern Mexico. Species preceded by an asterisk are exotic. Dispersal syndromes were assessed by structures attached to the seeds: none; presence of flesh associated with vertebrates (vert); elaiosomes (ants); adhesive structures (adh); explosive (exp), wings, plumes or other structures that increase wind resistance (wind). Life form was categorized into woody species (w); forbs (f) and grasses (g). Mean seed mass represents the mean of 20 seeds from at least 10 different plants

Species	Family	Dispersal	Lifeform	Season of seed collection	Mean seed mass (mg) \pm S.D.
<i>Acacia berlandieri</i> Benth.	Mimosaceae	none	w	Summer	327.000 \pm 27.428
<i>Acacia farnesiana</i> (L.) Willd	Mimosaceae	none	w	Summer	61.450 \pm 2.724
<i>Acacia rigidula</i> Benth.	Mimosaceae	none	w	Spring	24.970 \pm 1.910
<i>Acacia schaffneri</i> (Wats.)Herm.	Mimosaceae	none	w	Summer	82.060 \pm 7.110
<i>Acacia wrightii</i> Benth.	Mimosaceae	none	w	Summer	63.180 \pm 4.832
<i>Amaranthus palmeri</i> Wats.	Amaranthaceae	none	f	Winter	0.345 \pm 0.031
<i>Amyris madrensis</i> Wats.	Rutaceae	vert	w	Autumn	250.990 \pm 32.997
<i>Amyris texana</i> (Buckl.) P. Wils.	Rutaceae	vert	w	Autumn	11.980 \pm 0.798
<i>Aristida adscensionis</i> L.	Poaceae	wind	g	Winter	1.535 \pm 0.079
<i>Asclepias oenotheroides</i> Scheele	Asclepiadaceae	wind	f	Summer	3.620 \pm 0.140
<i>Astrophytum asterias</i> (Zucc.) Lem.	Cactaceae	vert	f	Summer	1.383 \pm 0.119
<i>Boerhavia coccinea</i> Mill.	Nyctaginaceae	adh	f	Spring	0.966 \pm 0.351
<i>Bouteloua curtipendula</i> Lag.	Poaceae	none	g	Autumn	0.330 \pm 0.070
<i>Caesalpinia mexicana</i> Gray	Caesalpiniaceae	exp	w	Autumn	46.830 \pm 3.235
<i>Calea ternifolia</i> Kunth	Asteraceae	wind	f	Winter	0.338 \pm 0.022
<i>Calliandra conferta</i> Benth.	Mimosaceae	none	t	Summer	29.125 \pm 2.756
<i>Capsicum annuum</i> var. <i>minus</i> (Fing.) Shinnery	Solanaceae	vert	f	Autumn	1.185 \pm 0.079
<i>Cardiospermum halicacabum</i> L.	Sapindaceae	wind	t	Autumn	25.510 \pm 3.186
<i>Castela erecta</i> Turp ssp. <i>texana</i> (T. & G.) Cronq.	Simaroubaceae	vert	w	Summer	82.610 \pm 5.895
<i>Celtis iguanea</i> (Jacq.) Sarg.	Ulmaceae	vert	w	Spring	5.850 \pm 0.963
<i>Celtis laevigata</i> Willd.	Ulmaceae	vert	w	Autumn	99.170 \pm 4.100
<i>Celtis pallida</i> Torr.	Ulmaceae	vert	w	Winter	27.940 \pm 1.735
<i>Cenchrus incertus</i> M.A. Curtis	Poaceae	adh	g	Spring	4.980 \pm 0.826
<i>Cercidium macrum</i> I.M. Johnst.	Caesalpiniaceae	none	w	Summer	82.383 \pm 6.637
<i>Chamaecrista greggii</i> var. <i>greggii</i> (Moench.)I. & B.	Caesalpiniaceae	none	w	Autumn	13.895 \pm 1.166
<i>Chloris cucullata</i> Bisch.	Poaceae	wind	g	Summer	0.036 \pm 0.003
<i>Chloris gayana</i> Kunth	Poaceae	wind	g	Autumn	0.328 \pm 0.020
<i>Cissus sicyoides</i> L.	Vitaceae	vert	t	Autumn	52.675 \pm 7.018

<i>Citharexylum berlandieri</i> Robins.	Verbenaceae	vert	w	Spring	40-095 ± 5-296
<i>Colubrina greggi</i> Wats.	Solanaceae	none	w	Winter	39-250 ± 2-719
<i>Condalia hookeri</i> M.C. Johnst.	Rhamnaceae	vert	w	Summer	17-115 ± 1-381
<i>Cordia boissieri</i> A.DC.	Boraginaceae	vert	w	Summer	591-460 ± 51-283
<i>Croton ciliatoglandulifer</i> Ort.	Euphorbiaceae	ant	f	Winter	9-667 ± 2-214
<i>Croton cortesianus</i> H.B.K.	Euphorbiaceae	ant	f	Winter	5-825 ± 1-228
<i>Croton torreyanus</i> Muell. Arg.	Euphorbiaceae	ant	f	Autumn	5-095 ± 0-580
<i>Cynanchum barbigerum</i> (Sheele) Shinners.	Asclepiadaceae	wind	t	Autumn	1-550 ± 0-254
<i>Desmanthus virgatus</i> (L.) Willd.	Mimosaceae	none	f	Summer	4-150 ± 0-473
<i>Diospyros palmeri</i> Scheele	Ebenaceae	vert	w	Autumn	253-520 ± 19-299
<i>Diospyros texana</i> Scheele	Ebenaceae	vert	w	Summer	116-880 ± 5-517
<i>Diphysa minutifolia</i> Gray	Fabaceae	none	f	Summer	11-283 ± 1-521
<i>Ebenopsis ebano</i> (Berl.) Barneby & Grimes.	Mimosaceae	exp	w	Summer	597-636 ± 132-517
<i>Ehretia anacua</i> (Teran & Berl.) I.M. Johnst.	Boraginaceae	vert	w	Summer	67-433 ± 8-934
* <i>Eragrostis curvula</i> (Schrud.) Nees	Poaceae	none	g	Winter	0-072 ± 0-017
<i>Eragrostis neomexicana</i> Vasey.	Poaceae	none	g	Winter	0-062 ± 0-012
<i>Eupatorium havanense</i> H.B.K.	Asteraceae	none	f	Winter	0-256 ± 0-011
<i>Euphorbia dentata</i> Michx.	Euphorbiaceae	none	f	Summer	1-105 ± 0-120
<i>Euphorbia hexagona</i> L.	Euphorbiaceae	ant	f	Summer	3-410 ± 0-272
<i>Evokulus alsinoides</i> L.	Convulvulaceae	none	f	Summer	0-669 ± 0-116
<i>Eysenhardtia polystachya</i> Scheele	Fabaceae	none	w	Winter	5-220 ± 0-268
<i>Eysenhardtia texana</i> Scheele	Mimosaceae	none	w	Winter	2-730 ± 0-162
<i>Galactia brachystachya</i> Benth.	Fabaceae	exp	t	Winter	34-610 ± 4-310
<i>Galactia texana</i> Scheele	Fabaceae	exp	t	Autumn	23-450 ± 1-664
<i>Gochmatia hypoleuca</i> DC.	Asteraceae	wind	w	Winter	0-268 ± 0-043
<i>Gonolobus gonoloboides</i> Benth.	Asclepiadaceae	wind	t	Spring	5-180 ± 0-663
<i>Gonolobus</i> sp1	Asclepiadaceae	wind	t	Autumn	17-030 ± 0-778
<i>Gonolobus</i> sp2	Asclepiadaceae	wind	t	Spring	5-780 ± 0-428
<i>Guaiacum angustifolium</i> Engelm.	Zygophyllaceae	vert	w	Autumn	97-667 ± 17-559
<i>Gymnosperma glutinosum</i> (Spreng.) Less.	Asteraceae	wind	f	Winter	0-118 ± 0-011
<i>Havardia pallens</i> (Benth.) Brit. & Rose	Fabaceae	none	w	Autumn	42-795 ± 3-774
<i>Hedeoma drummondii</i> Benth.	Lamiaceae	wind	f	Summer	0-049 ± 0-010
<i>Helianthus annuus</i> L.	Asteraceae	none	f	Summer	5-055 ± 0-408
<i>Helietta parvifolia</i> (Gray) Benth.	Rutaceae	wind	w	Autumn	19-760 ± 2-925
<i>Heliotropium curassavicum</i> L.	Boraginaceae	none	f	Summer	3-820 ± 0-374
<i>Herisantia crispa</i> Harv.	Malvaceae	none	f	Winter	9-350 ± 0-760
<i>Hibiscus cardiophyllus</i> Gray	Malvaceae	none	f	Summer	8-105 ± 0-246

Appendix 1.—Continued

Species	Family	Dispersal	Lifeform	Season of seed collection	Mean seed mass (mg) \pm S.D.
<i>Hibiscus coulteri</i> Harv.	Malvaceae	none	f	Summer	2·870 \pm 0·279
<i>Karwinskia humboldtiana</i> (R. & S.) Zucc.	Rhamnaceae	vert	w	Autumn	57·540 \pm 7·996
<i>Lantana macropoda</i> Torr.	Verbenaceae	none	f	Summer	3·740 \pm 0·510
<i>Lantana velutina</i> Torr.	Verbenaceae	none	f	Summer	11·460 \pm 1·622
<i>Leucophyllum frutescens</i> (Berl.) I.M. Johnst.	Scrophulariaceae	none	w	Summer	0·057 \pm 0·009
<i>Malpighia glabra</i> L.	Malpighiaceae	vert	w	Summer	22·925 \pm 0·918
<i>Malvastrum coromendelianum</i> (L.) Gke.	Malvaceae	none	f	Autumn	1·240 \pm 0·097
<i>Mascagnia macroptera</i> Kunth	Malpighiaceae	wind	t	Winter	38·683 \pm 5·902
<i>Maximalva filipes</i> (Gray) Fryxell	Malvaceae	none	f	Autumn	1·950 \pm 0·107
<i>Melochia tomentosa</i> L.	Sterculiaceae	none	f	Summer	1·015 \pm 0·165
<i>Mimosa monancistra</i> Benth.	Mimosaceae	none	w	Autumn	31·967 \pm 2·714
<i>Neopringlea integrifolia</i> (Hemsl.) Wats.	Flacourtiaceae	wind	w	Winter	1·770 \pm 0·217
<i>Nicotiana glauca</i> Grah.	Solanaceae	vert	f	Summer	0·031 \pm 0·004
* <i>Parkinsonia aculeata</i> L.	Caesalpiniaceae	none	w	Summer	112·070 \pm 4·842
<i>Passiflora foetida</i> L.	Passifloraceae	vert	t	Summer	4·950 \pm 0·892
<i>Pavonia lasiopetala</i> Scheele	Malvaceae	none	f	Summer	0·230 \pm 0·015
* <i>Pennisetum ciliare</i> (L.) Link	Poaceae	wind	g	Spring	0·700 \pm 0·084
<i>Phaulothamnus spinescens</i> Gray	Phytolaccaceae	vert	w	Autumn	5·650 \pm 0·273
<i>Physalis viscosa</i> L.	Solanaceae	vert	f	Summer	0·445 \pm 0·059
<i>Prosopis laevigata</i> (Willd.) M.C. Johnst.	Mimosaceae	vert	w	Summer	54·780 \pm 4·084
<i>Randia rhagocarpa</i> H.B.K.	Rubiaceae	vert	w	Summer	92·650 \pm 11·234
* <i>Rhynchelytrum repens</i> (Willd.) C.E. Hubb.	Poaceae	wind	g	Summer	0·200 \pm 0·010
<i>Ruellia nudiflora</i> (Gray) Urban	Acanthaceae	wind	f	Spring	1·417 \pm 0·393
<i>Salvia ballotaeflora</i> Benth.	Lamiaceae	wind	f	Summer	0·540 \pm 0·070
<i>Salvia coccinea</i> Juss.	Lamiaceae	wind	f	Spring	0·830 \pm 0·056
<i>Sanvitalia ocymoides</i> DC.	Asteraceae	wind	f	Summer	0·305 \pm 0·019
<i>Scutellaria drummondii</i> Benth.	Lamiaceae	wind	f	Summer	0·575 \pm 0·083
<i>Schaefferia cuneifolia</i> Gray.	Celastraceae	vert	w	Autumn	5·915 \pm 0·721
<i>Sida neomexicana</i> Gray.	Malvaceae	none	f	Winter	2·375 \pm 0·209
<i>Sideroxylon celastrinum</i> (Kunth) Penn.	Sapotaceae	vert	w	Spring	67·720 \pm 5·639
<i>Simsia calva</i> (Engelm. & Gary) Gray	Asteraceae	wind	f	Summer	1·210 \pm 0·104
<i>Smilax pumila</i> Watt.	Smilacaceae	vert	t	Summer	12·400 \pm 1·945

<i>Solanum erianthum</i> D. Don.	Solanaceae	vert	f	Summer	0.775 ± 0.054
<i>Solanum rostratum</i> Dun.	Solanaceae	vert	f	Summer	4.440 ± 0.242
* <i>Sorghum halepense</i> (L.) Pers.	Poaceae	wind	g	Summer	5.620 ± 0.485
<i>Teucrium cubense</i> Jacq.	Lamiaceae	none	f	Summer	1.490 ± 0.184
<i>Thelosiphonia macrosiphonia</i> (Torr.) Henderson	Apocynaceae	wind	f	Autumn	4.400 ± 1.960
<i>Thymophylla pentachaeta</i> (Willd.) Strother	Asteraceae	wind	f	Summer	0.144 ± 0.050
<i>Tournefortia volubilis</i> L.	Boraginaceae	vert	f	Summer	10.040 ± 1.315
<i>Tragia ramosa</i> Torr.	Euphorbiaceae	none	f	Summer	11.850 ± 1.784
<i>Tridax coronopifolia</i> (H.B.K.) Hemsl.	Asteraceae	wind	f	Summer	0.758 ± 0.048
<i>Urvillea ulmacea</i> Kunth	Sapindaceae	none	t	Summer	6.460 ± 0.651
<i>Verbena canescens</i> H.B.K.	Verbenaceae	wind	f	Summer	0.765 ± 0.055
<i>Verbesina olseni</i> Gray	Asteraceae	wind	f	Autumn	0.347 ± 0.038
<i>Viguiera stenoloba</i> Blake.	Asteraceae	wind	f	Summer	0.342 ± 0.076
<i>Zenthoxylum fagara</i> (L.) Sarg.	Rutaceae	vert	w	Autumn	6.120 ± 0.631
