REGULAR PAPER

Relationship between seed size and related functional traits in North Saharan *Acacia* woodlands

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Background and aims – North Saharan *Acacia* woodland is a fragile ecosystem altered by desertification and human activities. Little research has been conducted on the ecology of North Saharan *Acacia* woodland species. Seed size is a key trait to determine germination success, survival rate and establishment of *Acacia* woodland species under desert constraints.

Methods – We analysed seed-size relationships in 42 selected woody plants in four different types of *Acacia* woodland vegetation which correspond to 26 plant species. We examined the correlation among seed size, fruit size, plant height, leaf size and flowering time and we tested seed size and fruit size variation among growth forms, dispersal modes and mechanisms to prevent dispersal.

Key results – Close relationships were found between seed size and fruit size ($r = 0.77**$), between fruit size and plant height ($r = 0.51**$) and between seed size and flowering duration ($r = -0.46*$) and a weak positive relationship was found between fruit and leaf size. Species with restricted spatial dispersal tended to have smaller seeds and fruits compared to those with well-developed spatial dispersal. Species which disperse and germinate throughout the year tended to have large diaspores, whereas species with seasonal germination tended to have small diaspores. The relationship between seed size and growth form/plant height was strong for gravity-dispersed (barochorous) species secondarily dispersed by vertebrates (*Ziziphus lotus*), seeds with secondary wind-assisted dispersal (*Zilla spinosa* subsp. *macroptera*) and for restricted-dispersal species (*Tetraena gaetula*). Precocious, short-flowering species that spread dispersal and germination over time (*Acacia tortilis* subsp. *raddiana*) tended to have large seeds. Early- and long-flowering herbaceous species tended to have small seeds (*Brocchia cinerea*).

Conclusion – Close relationships are found between seed size and fruit size, between fruit size and plant height and between seed size and flowering duration in Moroccan *Acacia* woodland species.

Key words – *Acacia* woodlands, dispersal, flowering phenology, leaf size, Morocco, plant height, seed size.

INTRODUCTION

Seed size, leaf size and plant height appear to be fundamental and integrating properties of species that reflect most of the total variation in plant function (Westoby 1998) and are the focal attributes in particularly important plant strategy dimensions (Wright et al. 2007). Seed size (together with plant height), is one of the best traits for describing plant fitness (Weiher et al. 1999) because increased seed size increases the probability of successful seedling establishment (Westoby et al. 2002) and increases the probability of plant persistence (Moles et al. 2005).

Plant attributes are commonly inter-correlated (Wright et al. 2007). Seed size is positively correlated with plant height (Wright et al. 2007) and fruit size (Wright et al. 2007). Within species, seed size is often associated with specific growth forms (Mazer 1989, Jurado et al. 1991), dispersal modes, and mechanisms to prevent dispersal (Ellner & Shmida 1981, Jurado et al. 1991, Navarro et al. 2009a, 2009b). Prevented-dispersal species are more adapted to arid and desert habitats by the protection of the seeds from predation and other dangers, and sensitive regulation of the within and between-year timing of dispersal and germination (van Rooyen et al. 1990, van Rheede van Oudtshoorn & van Rooyen 1999, Gutterman 2001). Flowering time represents the phenological behaviour by which plants begin allocating resources from their own growth and survival to reproduction and offspring development (Bolmgren & Cowan 2008), which affect reproduc-

tive success (McIntosh 2002). In desert plants, phenological events, especially flowering time, are triggered mainly by variation in rainfall, soil water availability and suitable temperature (Noy-Meir 1973, Bowers & Dimmitt 1994). Seed size is correlated with flowering time (Mazer 1989). Earlier flowering allows for a longer development time of seeds, which promotes larger seeds (Mazer 1990). Later flowering implies that more resources are available for seed development but a shorter time is available for seed maturation and dispersal (Roux et al. 2006). We expect that flowering time of species in North Saharan woodlands can represent a fundamental trade-off between the outcome of the parent (size) and offspring development time (Bolmgren & Cowan 2008). We focused on a North Saharan *Acacia* woodland formation because it constitutes a scattered desert sub-tropical vegetation exclusive to habitats with limited resources, as dry valleys (wadis), still being rapidly altered by desertification and human activities in Morocco (Quézel 1965, Yassin et al. 2002, 2005). Although numerous empirical studies have been conducted with regard to seed size (Weiher et al. 1999), no information on how they are associated with the related plant traits of North Saharan *Acacia* woodlands is available.

Under these conditions, we examined if the variation of seed and fruit size among growth forms, dispersal modes, spatial dispersal and mechanisms to prevent dispersal on North Saharan *Acacia* woodlands were consistent with those reported previously in other arid regions (Navarro et al. 2006, 2009a, 2009b). We also tested the effect of duration of flowering time on seed size, which depends upon the time when flowering begins (Wulff 1986, Mazer 1989, Bolmgren & Cowan 2008). We wanted to investigate a hypothesised relationship between seed size and plant allometric attributes measured in Moroccan North Saharan *Acacia* woodlands. Our predictions were as follows:

(1) Fruit size constrains the maximum possible size of seeds. Small-fruited species would have small seeds only, and for the very smallest fruits, the seed size and fruit size would be almost identical, whereas large-fruited species would have a wider range of seed sizes (Wright et al. 2007).

(2) Seed size-fruit size would be positively correlated with plant height (Wright et al. 2007).

(3) A triangular relationship between seed size and leaf size would be weakly significant (small-seeded species would have small leaves only, whereas larger-seeded species would have a relatively wide range of leaf sizes; Cornelissen 1999). This triangular relation forms part of the ecological strategy defined for terrestrial plants on the basis of the Corner allometric "rules" (Corner 1949).

MATERIALS AND METHODS

Study area

North Saharan desert occurs between Egypt and Mauritania. Cooler winter rains sustain dry sub-tropical woodlands and shrublands that form a transition zone between the Mediterranean climate regions to the north and the sub-tropical Sahara proper to the south (White 1983). Throughout most of the eco-region there are very few and small areas of permanent vegetation. Where this occurs, it is confined to sand dunes, stone plateaux, gravel plains, dry valleys or salt flats

(Cloudsley-Thompson 1984). The flora of these areas is very poor and estimated to include less than 500 species (WWF & IUCN 1994). This is extremely low considering the huge extent of the area (1 675 300 km² – WWF & IUCN 1994).

North Saharan Moroccan *Acacia* woodlands are a fragile desert sub-tropical ecosystem (Yassin et al. 2002, 2005) undergoing desertification, a deteriorating transition from semi-arid to desert ecosystems. The disruptive effects of man and droughts intensify the disappearance of perennial species, mainly *Acacia* trees and large shrubs, in certain zones (Yassin et al. 2002, 2005), and consequently a concomitant reduction in biological productivity and biodiversity (Le Houérou 1997). The study was conducted in the North Saharan Moroccan *Acacia* woodlands (Quézel 1965, Quézel et al. 1994, Yassin et al. 2002, 2005) extending c. 700 km² between 600 and 850 m a.s.l. in south-western Morocco (Zagora and Ouarzazate districts). A total of 550 km² of our study area are integrated in the Oued Mird Observatory of ROSELT (Réseau d'Observatoires de Surveillance Ecologique à Long Terme - Network of Longterm Ecological Monitoring Observatories) / Observatoire du Sahara et du Sahel (OSS Sahara and Sahel Observatory). The climate is defined as semi-arid (Le Houérou 1997), characterized by a long drought period extending the whole year and weak rains (end of autumn and beginning of winter and spring), with wind and sand storms occurring as early as the beginning of spring. The 50-year (1933–1963) mean maximum and minimum temperatures are 43 and 2.5°C, respectively. Mean annual precipitation is 13.5 mm (1998–2002) (Yassin et al. 2002). The vegetation corresponds to the *Zizipho loti–Acacietum raddianae* (Quézel 1965) association. Three types were distinguished according to *Acacia tortilis* subsp. *raddiana* (Savi) Brenan tree density (as *Acacia raddiana*: Yassin et al. 2002, 2005), and one without *Acacia* trees:

- an open *Acacia* woodland (2 trees/ha: 21.55 ha; resprouted *Acacia* trees that do not reach maturity) (30°08′08″N, 5.38°9′94″W) with an open canopy of 20–30%, on the flat upper slopes over rocky-clay limestone and sandy substrate (AEFCS 1996);
- a medium-dense to dense *Acacia* woodland (7 trees/ha: 5.57 ha) (30°9′56″N, 5°20′23″W) with a canopy of 40–50% on the flat surfaces over limestone sandy substrate;
- a dense *Acacia* woodland (18 trees/ha: 4.23 ha) (30°07′28″N, 5°11′53″W) with a closed canopy of 60% over rocky sites with accumulation of sand;
- a *Ziziphus lotus* woodland without *Acacia* trees (30°76′63″N, 6°69′29″W) with a canopy of 40–60% over rocky limestone substrate.

Species selection

We selected 12 sites throughout the study area, aiming to sample a cross-section of North Saharan *Acacia* woodlands in Morocco (Quézel et al. 1994, Yassin et al. 2002, 2005). Of the 12 sites, six corresponded to open *Acacia* woodland, two were medium-dense, three were dense and one corresponded with the *Ziziphus lotus* shrub woodland. Species dominance had been previously assessed with relative importance values (Yassin et al. 2002, 2005) in which species abundance has been estimated according to the Braun-Blanquet scale

(Braun-Blanquet 1952). A total of 42 woody plants (trees and shrubs), both deciduous and evergreen, and perennial herbaceous species were selected from all the studied sites which correspond to 26 different species. These 26 selected species represent 80.6% of total perennial species (excluding graminoids) that integrate the North Saharan Moroccan *Acacia* woodlands (Yassin et al. 2002, 2005). All 26 taxa are presented in electronic appendix. Nomenclature of the families follows APG IV (Angiosperm Phylogeny Group 2016) and nomenclature of the species follows Euro+Med PlantBase (Euro+Med 2006–2018).

Trait measurements

Field sampling and trait observations were carried out from 2008 to 2010. We analysed ten plant attributes (electronic appendix), following protocols described in Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013).

Trees and shrubs were phanerophyte species, half-shrubs were chamaephytes and perennial herbs were hemi-cryptophytes. Plant height was measured on 25 adult individuals per species. *Acacia* tree height was based on Yassin et al. (2002).

To calculate leaf size (leaf area) we collected 20 sun leaves from 10 well developed individual plants. Leaf measurements (leaf area) of each individual leaf were estimated using Visilog 6.0 image analysis software in the Central Support Research Services (SCAI) of the University of Malaga. For the leaf size classes, the classification of Raunkaier as modified by Orshan (1982) was applied. The term 'diaspore' was used to name the dispersal unit (seed or fruit) (Weiher et al. 1999). If a fruit is dehiscent, the dispersal unit is usually the seed. Indehiscent fruits do not open to release their seeds. In these cases, the seeds are distributed together with the entire fruit or part of the fruit. Two categories were used: species dispersed by seed or entire fruit.

To measure diaspore size, diaspores were collected when ripe but before they started to fall off the plant. For each individual and each site, 20 diaspores (100 for small-seeded species) were air-dried and measured. We considered that species with developed spatial dispersal are those whose diaspores are equipped with wings (dispersed by abiotic vectors) or fleshy fruits (dispersed by biotic vectors) according to Ellner & Shmida (1981). We considered species with restricted spatial dispersal those whose diaspores lack such dispersal-enhancing characters, following Willson (1993).

The mechanisms to prevent primary or secondary dispersal (van Rheede van Oudtshoorn & van Rooyen 1999) include bradyspory (the gradual release of seed from a fruit over a long period of time), hygrochasy (the opening of a fruit caused by water or moisture), trypanocarpy (dispersed fruit turning around, creeping or drilling by hygroscopic movement) and basicarpy (compact inflorescences are produced close to the soil surface, the diaspores remain attached to the dead mother plant, and the dead mother is held in place by a strong lignified root (van Rooyen et al. 1990), synaptospermy (two or more seeds or one-seeded fruits) are joined together to form a compound diaspora (Ellner & Shmida 1981, van Rooyen et al. 1990) and myxospermy (ability of a seed to produce mucilage upon hydration (van Rooyen et al. 1990).

The mechanisms regulating the within-season timing of germination and diaspore anchorage against surface runoff are hygrochasy, myxospermy, basicarpy and trypanocarpy; and the mechanisms spreading dispersal and germination over time (several years) include synaptospermy and bradyspory (electronic appendix). For the mechanisms that prevent dispersal, the observations were made directly in the field or in the laboratory (myxospermy). The traits were measured for each 26 selected species (electronic appendix).

Phenological surveys and flowering time

Phenological surveys were performed for at least two years, between December 2008 and July 2010. Each year, the units of vegetation were observed 8–12 times with intervals of approximately 30–45 days. Mean Julian flowering dates were recorded. Flowering duration for each species was determined using the first and last months that a species is in flower. For example, *Acacia tortilis* subsp. *raddiana* flowers from August until September of the following year which corresponds to the Julian days 212 through 273. Therefore, the mean Julian flowering day: $(212 + 273) / 2 = 242.5$ and the flowering duration: $273 - 212 = 61$ days. Onset of flowering was defined as follows:
- early: species begin to flower after the first main rains, in January or February;
- middle: species begin to flower in March or April with the second weak rainy period;
- late: species begin to flower in late spring or at the onset of the dry period, May–June;
- precocious: species begin to flower at the end of the dry summer period or at the onset of first rainy period (end of the autumn-winter rain) in July–December.

Duration of flowering was defined as follows:
- short: species flower during 1–2 months for only a short portion of a season;
- medium: species flower during 2–3 months or over an entire season;
- long: species that flower for 4 months or over the course of more than one season.
Flowering phenological verifications were carried out on RAB herbarium specimens. Voucher specimens of all the studied species were deposited in RAB (Herbarium of Rabat Scientific Institute, Morocco) and MGC (Herbarium of Málaga University, Spain). Species, family, growth form, leaf traits, whole-plant traits, seed and fruit size, dispersal traits and flowering time are presented in the electronic appendix.

Data analysis

Continuous characters were $\log_{10}$-transformed to reach normality prior to statistical analysis. Correlations between continuous traits (seed size, fruit size, plant height, leaf size and flowering time) were examined using Pearson correlation coefficient to test for significant differences ($p < 0.05$). The association between non-continuous traits was determined with the Pearson χ^2 test-statistic to test for significant differences ($p < 0.05$). One-way analysis of variance (ANOVA) and Bonferroni-corrected paired t-tests were used to test for significant differences ($p < 0.01$) among seed size, fruit size, plant height leaf size and growth forms, dis-

persal modes, spatial dispersal and mechanisms to prevent dispersal. The mean diaspore size (weight) of each species was also assigned to classes 4 to 12 devised by Baker (1972) (4: 0.32–0.099 mg; 5: 0.100–0.315 mg; 6: 0.316–0.999 mg; 7: 1.000–3.161 mg; 8: 3.162–9.999 mg; 9: 10.000–31.611 mg; 10: 31.612–99.999 mg; 11: 100.000–316.108 mg; 12: 316.109–999.999 mg). We performed a nonlinear principal components analysis (NLPCA) (Linting et al. 2007) using the program CATPCA implemented in the software SPSS 15.0. (SPSS. Inc. 2006) on six traits; seed size, fruit size, plant height, leaf size, flowering duration and date of flowering. One-way analysis of variance (ANOVA) and t-tests were applied after verifying the homogeneity of variance by Levene's test. All statistical analyses were performed with SPSS 15.0. The original matrices are available on request.

RESULTS

The species studied represent 24 genera and 13 families (electronic appendix). Sub-shrubs (chamaephytes) (44%)

were the dominant growth form, followed by perennial herbs (hemicryptophytes) (36%) and trees (phanerophytes) (20%).

Seed size (seed weight) ranged from 0.11 mg in *Linaria aegyptiaca* (middle-dense *Acacia* woodland) and 0.12 mg in *Caylusea hexagyna* (open *Acacia* woodland) to 91.19 mg in *Acacia tortilis* subsp. *raddiana* (middle-dense *Acacia* woodland), with a mean of 8.27 mg. Fruit size ranged from 0.05 mg in *Brocchia cinerea* (dense *Acacia* woodland) to 969.16 mg in *Acacia tortilis* subsp. *raddiana* (dense *Acacia* woodland). Fifty percent of species were dispersed by seed and 50% dispersed by fruit (electronic appendix). Small diaspores (Baker's classes 4 to 7) tended to have a greater abundance (48%) than larger-diaspore species (Baker's classes 8 to 12; 36%).

Leaf size ranged from 838.19 mm^2 in *Withania adpressa* (dense *Acacia* woodland) to 2.65 mm^2 in *Acacia tortilis* subsp. *raddiana* (middle-dense *Acacia* woodland) (electronic appendix) with a mean of 144.31 mm^2. The studied species spanned a 100-fold range of leaf sizes, from 10 to 1000 mm^2.
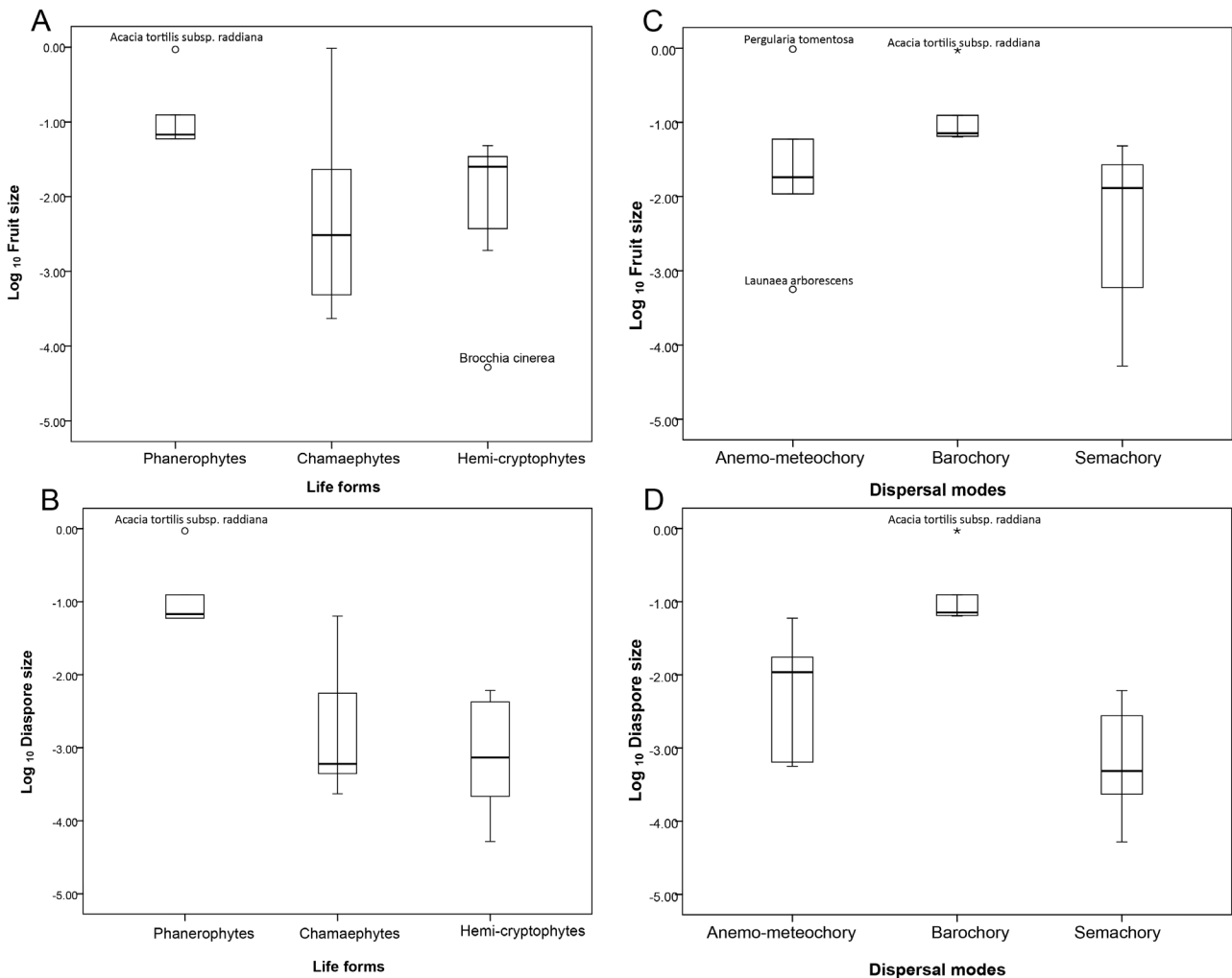

Figure 1 – Box plots showing median and quartiles of fruit size (A, C) and diaspore size (B, D) (log$_{10}$-transformed) of 26 perennial species in the North Saharan *Acacia* woodland of south-western Morocco grouped by growth forms (A, B) and dispersal modes (C, D). *Acacia tortilis* subsp. *raddiana*, *Brocchia cinerea*, *Pergularia tomentosa* and *Launaea arborescens* are the "outliers" species with values between 1.5 and 3 box lengths from the upper or lower edge of the box.

Nanophyll leaves (leaves 25–225 mm²) were over-represented (66.6%) in *Ziziphus lotus* woodlands.

Seed size-fruit size variation among *Acacia* woodlands

While seed size and fruit size did not differ significantly among the *Acacia* woodland formations ($p > 0.05$), larger diaspores (Baker's class 12) were found exclusively in dense and middle-dense *Acacia* woodland and correspond with the fruits of *Acacia tortilis* subsp. *raddiana*, *Zilla spinosa* subsp. *macroptera* and *Ziziphus lotus*. The small diaspores (50% of Baker's class 4; e.g. *Brocchia cinerea*) and the small-medium diaspores (37.5% of Baker's class 5; e.g. *Sideritis ochroleuca*) were predominant in open *Acacia* woodland.

Fruit and seed size variation among growth forms, spatial dispersal, dispersal modes and mechanisms to prevent (secondary) dispersal

The growth forms differed in fruit size ($F = 2.98$, df = 2, 25, $p < 0.01$, fig. 1A) and diaspore size ($F = 14.43$, df = 3, 24, $p < 0.01$, fig. 1B). Bonferroni-corrected pairwise comparisons only found significant differences ($p < 0.01$, fig. 1B) for diaspore size between trees vs. shrubs and trees vs. perennial herbs. Trees and large shrubs tend to have larger diaspores than small shrubs and perennial herbs (fig. 1B). Species with different dispersal capacities differed significantly in seed size and fruit size (*t*-test on $\log_{10}$-transformed data $p < 0.01$). Restricted-dispersal species tend to have smaller seeds and fruits than species with adaptations for dispersal.

Species with different dispersal modes differed in fruit size ($F = 4.90$, df = 2, 25, $p < 0.01$, fig. 1C) and diaspore size ($F = 21.17$, df = 2, 25, $p < 0.01$, fig. 1D). Bonferroni-corrected pairwise comparisons only found significant differences ($p < 0.01$, fig. 1C) for fruit size between barochorous (gravity dispersed) vs. semachorous (seed dispersal by movement caused by wind or animals passing) species and for diaspore size between barochorous vs. anemo-meteochorous (wind dispersed) and semachorous species. Barochorous species (Baker's classes 12, 11 and 10) had larger diaspores than anemo-meteochorous and semachorous species, and anemo-meteochorous species tended to have larger fruits and diaspores than semachorous species (Baker's class 4).

Species with different mechanisms to prevent dispersal differed in diaspore size ($F = 4.77$, df = 2, 25, $p < 0.01$), but not in seed and fruit size. Species spreading dispersal and germination over time tended to have larger diaspores (Baker's classes 12 and 11 were exclusive for these species) and species regulating the within-season timing of germination tended to have small diaspores (Baker's class 4).

Positive correlations of seed size with fruit size and plant height

The positive correlation was found between seed size and fruit size ($r = 0.77$, $p < 0.05$). Small seeds in medium fruits were found in herbaceous, restricted-dispersal species without a mechanism to prevent dispersal (e.g. *Caylusea hexagyna*, *Linaria aegyptiaca*). Medium seeds in larger fruits were species with developed spatial dispersal and with more than one mechanism to prevent secondary dispersal (e.g. *Cleome*

africana, *Tetraena gaetula* or *Zilla spinosa* subsp. *macroptera*). Large seeds in large fruits were found in species with spatial dispersal that spread dispersal and germination over time (e.g. *Ziziphus lotus*).

Across all species, there were four orders of magnitude of variation in seed size from 10^{-5} to 10^{-1} g and three orders of magnitude in fruit size from 10^{-4} to 10^{-1} g, while plant height ranged between 10^{-2} to 10^{-1} m. Fruit size was positively related with plant height ($r = 0.51$, $p < 0.05$). The large species with large fruits were secondary spatial dispersal species by vertebrates, e.g. *Withania adpressa*, *Ziziphus lotus*, and restricted dispersal species (e.g. *Tetraena gaetula*) regulating the within-season timing of germination. The medium species with large fruits were restricted-dispersal species without a mechanism to prevent secondary dispersal (e.g. *Convolvulus trabutianus*, *Reseda villosa*), and spatial-dispersal species spreading germination over time (e.g. *Zilla spinosa* subsp. *macroptera*, *Carthamus fruticosus*). The small species with large fruits were herbaceous, restricted-dispersal species (e.g. *Cleome africana*, *Fagonia* sp.). The small species with small fruits were shrubs with restricted dispersal (e.g. *Salvia aegyptiaca*, *Lavandula coronopifolia*, *Anvillea garcinii* subsp. *radiata*).

Larger-leaved species tend to have larger fruits

Leaf size varied over two orders of magnitude from 10^1 to 10^3 mm² and was marginally significantly related to fruit size ($r = 0.40$, $p < 0.05$). The species with small leaves and small fruits were restricted-dispersal Lamiaceae (e.g. *Salvia aegyptiaca*) and Asteraceae (e.g. *Brocchia cinerea*) species. The species with large leaves and large fruits were shrubs with spatial dispersal ability (e.g. *Withania adpressa*, *Zilla*
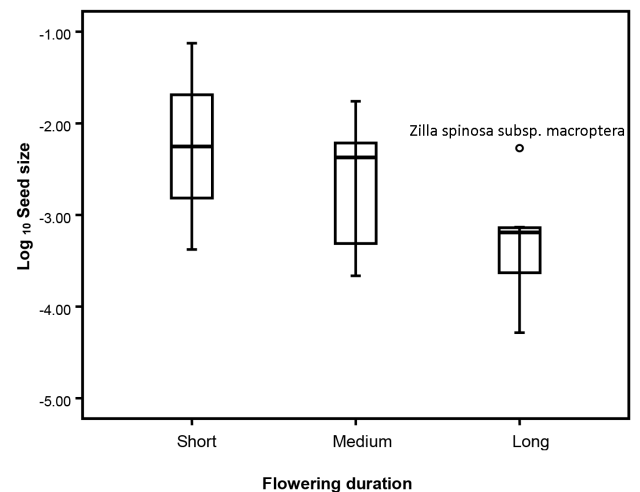

Figure 2 – Box plots showing median and quartiles of seed size ($\log_{10}$-transformed) of 26 perennial species in the North Saharan *Acacia* woodland of south-western Morocco grouped by flowering duration. Short: species flowering during 1–2 months; medium: species flowering during 2–3 months; long: species flowering during more than 4 months. *Zilla spinosa* subsp. *macroptera* is an "outliers" species with values between 1.5 and 3 box lengths from the upper or lower edge of the box.

Table 1 – Loading of the 6 traits on the first two components from Nonlinear Principal Components Analysis (NLPCA). Percentage of variance explained and Cronbach's Alpha are given for each component.

Traits	Components	
	1	2
Seed size	0.836	0.362
Fruit size	0.927	-0.186
Plant height	0.672	-0.288
Leaf size	0.329	-0.752
Flowering duration	-0.445	-0.510
Date of flowering	0.118	0.706
Variance explained	61.3	38.6
Cronbach's Alpha	0.685	0.436

spinosa subsp. *macroptera*, *Pergularia tomentosa*) except for the herbaceous restricted dispersers, *Moricandia arvensis* and *Reseda villosa*.

A negative correlation between seed size and flowering duration

Flowering duration was negative and significantly related to seed size ($r = -0.46$, $p < 0.05$). Short-flowering species (mean annual flowering = 77.60 days, 1–2 months) tended to produce larger seeds (Baker's classes 12 and 11) than species that displayed flowers for several months (fig. 2). These were mainly precocious shrub species spreading dispersal and germination over time (e.g. *Acacia tortilis* subsp. *raddiana*, *Carthamus fruticosus*). Long-flowering species (> 4 months, 124.14 days) with small seeds (Baker's class 4) were mainly earlier-flowering herbaceous species (e.g. *Brocchia cinerea*). Date of flowering was unrelated to seed and fruit size, but was significantly associated with diaspore type ($\chi^2 = 9.92$, df = 3, $p < 0.05$). All middle-flowering species were dispersed
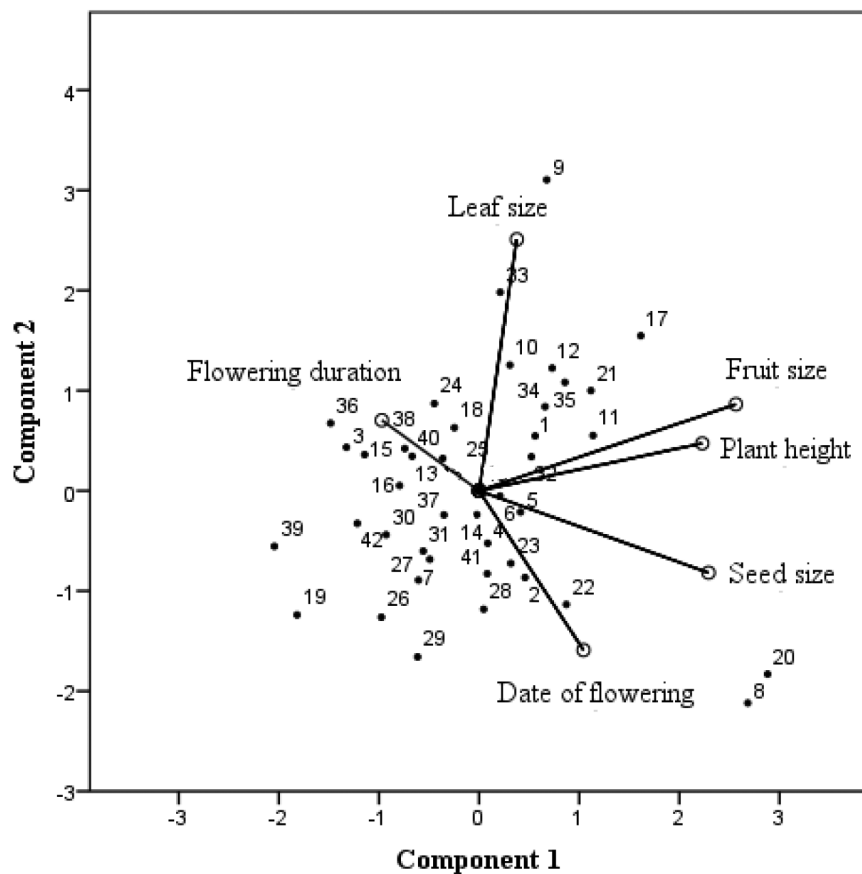

Figure 3 – Ordination plot of perennial species studied in the North Saharan *Acacia* woodland of south-western Morocco with component loading of the six analysed traits using Nonlinear Principal Components Analysis (NLPCA). Numbers indicate the species. 1, 12, 34: *Zilla spinosa* subsp. *macroptera*; 2, 22: *Convolvulus trabutianus*; 3, 15, 36: *Linaria aegyptiaca*; 4: *Farsetia occidentalis*; 5: *Euphorbia calyptrata*; 6, 32: *Cleome africana*; 7, 31: *Fagonia glutinosa*; 8, 20: *Acacia tortilis* subsp. *raddiana*; 9: *Withania adpressa*; 10, 25, 37: *Reseda villosa*; 11, 21: *Ziziphus lotus*; 13, 40: *Caylusea hexagyna*; 14, 23: *Farsetia aegyptia*; 16, 38, 42: *Anvillea garcinii* subsp. *radiata*; 17: *Pergularia tomentosa*; 18: *Tetraena gaetula*; 19, 39: *Brocchia cinerea*; 24: *Scrophularia ramosissima*; 26: *Salvia aegyptiaca*; 27: *Lavandula coronopifolia*; 28: *Carthamus fruticosus*; 29: *Sideritis ochroleuca*; 30: *Launea arborescens*; 33: *Moricandia arvensis*; 35: *Retama raetam*; 41: *Fagonia zilloides*.

by seeds whereas precocious and earlier species tended to be dispersed by fruits.

Multivariate analysis

The first two principal components accounted for 99.9% of the variation in the data (table 1, fig. 3). The first component explained 61.3% of the total variation and was most strongly correlated with fruit size, seed size and plant height. The second component explained 38.6% of total variation, and was negatively correlated with leaf size and flowering time. The first component (fig. 3) reflects a gradient in seed and fruit size, at one extreme the species with small seeds, small leaves, restricted spatial dispersal, without a mechanism to prevent dispersal and with earlier and longer flowering duration (e.g. *Linaria aegyptiaca*, *Brocchia cinerea*) and at the end of the component the larger species, with larger leaves, large fruits and developed spatial dispersal, mechanisms to prevent (secondary) dispersal and short-medium flowering duration (e.g. *Ziziphus lotus*, *Zilla spinosa* subsp. *macroptera*, *Carthamus fruticosus*).

DISCUSSION

The results of our study indicate that the pattern between seed size and other relevant plant functional attributes found by Wright et al. (2007), Cornelissen (1999) and Mazer (1989) is found also in our study region. The diaspore size range for perennial species from the North Saharan *Acacia* woodlands coincided with the range found in other arid and semi-arid ecosystems (Jurado et al. 1991, 2001, Leishman et al. 2000, Navarro et al. 2006, 2009a). However, in North Saharan *Acacia* woodlands there were no very small (10^{-6}) or very large (10^2) diaspores. The largest diaspores were found in the Fabaceae, while the smallest diaspores were found in the Scrophulariaceae, Lamiaceae and Asteraceae, in agreement with Mazer (1989). Interestingly, an important point indicated by our study is the close relationships between seed size and fruit size, between fruit size and plant height and between seed size and flowering duration.

Growth form, plant height and dispersal mode are the only attributes known to be correlated with substantial variation in seed size (Leishman et al. 2000). Dispersal mode is associated with seed size (Jurado et al. 1991) and a positive correlation between seed size and plant height has been reported consistently (Leishman et al. 2000). According to this, an interesting result indicated by our study is that the relationship between seed size and growth form/plant height is just as strong for large barochorous shrubs (phanerophytes) secondarily dispersed by vertebrates (e.g. *Ziziphus lotus*, *Whitania adpressa*, *Acacia tortilis* subsp. *raddiana*), with restricted dispersal (e.g. *Tetraena gaetula*), and secondarily wind assisted (e.g. *Zilla spinosa* subsp. *macroptera*, *Retama raetam*).

In North Saharan *Acacia* woodlands, species with mechanisms that prevent dispersal were predominant (60%), according to Ellner & Shmida (1981), van Rheede van Oudtshoorn & van Rooyen (1999), and Navarro et al. (2006, 2009a). Our results show that species that spread dispersal and germination over time tend to have larger diaspores

(Baker's classes 12 and 11), whereas species regulating the within-season timing of germination tend to have smaller diaspores (Baker's class 4). The large-seeded species tend to be superior colonists on sandy soils, because large seeds have greater potential to resist long-distance dispersal (van Rheede van Oudtshoorn & van Rooyen 1999), and provide improved germination and establishment (Silberbauer-Gottsberger 1984). This explains the large round fruits of pioneer species (e.g. *Retama raetam*, *Ziziphus lotus*) and typical xerophytic species (e.g. *Zilla spinosa* subsp. *macroptera* and *Tetraena gaetula*). In our study area, species regulating the within-season timing of germination tend to have small diaspores and small plant height (van Rheede van Oudtshoorn & van Rooyen 1999, Navarro et al. 2006, 2009a) and were herbaceous or woody, early- successional Asteraceae and Lamiaceae species (e.g. *Brocchia cinerea*, *Anvillea garcinii* subsp. *radiata*, *Salvia aegyptiaca*), which are common in arid ecosystems (Navarro et al. 2006, 2009a, 2009b) favoured by desertification processes in the most exposed sites (Yassim et al. 2002).

In our study area, a negative correlation was found between flowering time (duration) and seed size. A possible explanation for these relationships is a link via allocation resources for maternal plant growth and available resources for seed maturation and dispersal (Mazer 1989, Roux et al. 2006, Bolmgren & Cowan 2008). Species which have short flowering times produce significantly larger seeds than species which display flowers for several months (Primack 1987). Larger seeds require a longer development time, which leads to earlier flowering time when the growth period is limited. In North Saharan *Acacia* woodlands, the growth period is limited by extended dryness. Short flowering species (mean annual flowering = 77.60 days) with large seeds (Baker's classes 11 and 12) were consequently precocious trees and shrubs (e.g. *Acacia tortilis* subsp. *raddiana*, *Carthamus fruticosus*) with vegetative and reproductive phases separated by a dormant phase (summer drought period) so that flowers appear (Bolmgren et al. 2003). Results of the multivariate analysis synthesize information showing the main trends of species and their variation between sites. There are two groups of key species; those with small seeds, small leaves, restricted dispersal, without mechanisms to prevent dispersal and with earlier and longer flowering duration (e.g. *Linaria aegyptiaca*, *Brocchia cinerea*) from *Ziziphus lotus* formation without *Acacia* trees; and the larger shrubs, larger leaves, large fruits and developed spatial dispersal with mechanisms to prevent dispersal and short-medium flowering duration (e.g. *Zilla spinosa* subsp. *macroptera*, *Tetraena gaetula*, *Withania adpressa*) from middle-dense and dense *Acacia* formations. The results suggest that seed size variation is associated with other plant attributes according with Westoby et al. (1992). Species from *Acacia* woodland have found a diversity of possible solutions to the problems of seedling establishment, resulting in a wide range of seed masses (Leishman et al. 1995).

SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data) and consist of a

table with the scientific name, family and studied traits for each of the 26 studied species in four different vegetation types selected in the North Saharan *Acacia* woodlands of south-western Morocco.

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