

Dispersal traits in the hyper-arid hot desert of the United Arab Emirates

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Background and aims – This study describes the dispersal traits of 302 species in five Afro-Arabian habitats from the hyper-arid hot desert of United Arab Emirates (UAE).

Methods – Diaspore size (diaspora length) was studied in relation to growth forms, dispersal modes, presence of structures for long distance dispersal, APG IV groups, phytogeography and dispersal phenology using ANOVA and Pearson χ^2 test-statistical analyses.

Results – Small diaspores were predominant (six orders of magnitude from 10^{-4} to 10^2). The major diaspores were found in Fabids phylogenetic APG IV group (1.80 ± 0.41 cm) mainly trees and the minor in Commelinids (0.30 ± 0.08 cm). The most dominant dispersal mode was semachory (43.7% of the total and 67.5% of the herbaceous species), followed by anemo-meteochory (28.8%) and barochory (23.8%). Semachores/barochores (67.5%) formed the largest groups from the Fabaceae, Poaceae, Boraginaceae, Brassicaceae and Amaranthaceae families. Savanna trees such as *Acacia*, *Prosopis*, *Ziziphus* sp. and *Indigofera* sp. produced large diaspores secondarily dispersed by vertebrates. Anemo-meteochoric species with small diaspores were predominantly semi-shrubs such as *Haloxylon* sp. Graminoids such as *Stipa* sp. and *Stipagrostis* sp., without structures for long-distance dispersal had diaspore appendages acted as “active drills” in soil cracks. Dryness (dry season) favours the efficient dispersion by the wind for the small shrub species with haired capsule (e.g. *Aerva javanica*), winged calyx (e.g. *Astragalus squarrosus*) or wings (e.g. *Tribulus qatariensis*). Most of the species studied (64.2%) dispersed in the dry season according to what was found in other arid region from the world. The longer dispersal phenology corresponded to Saharo-Arabian and Sudano-Decanian species which is related to the floristic richness of the study area. Species dispersal throughout the year indicates an important seed resource e.g. barochoric species with fleshy fruits or pods with nutrient structures (e.g. *Senna italica* and *Indigofera* sp.).

Conclusions – In the hyper-arid hot desert of UAE, the dispersal spectra are close to those recorded in other arid environments but with particularities due to the presence of African floristic elements.

Key words – Dispersal spectrum, dispersal traits, diaspore size, hyper-arid hot desert.

INTRODUCTION

Plant dispersal plays an essential role in the colonization of new habitats, population dynamics as well as in species interactions and community structure and floral diversity (van der Pijl 1969, Howe & Smallwood 1982, Willson et al. 1990, Hughes et al. 1994, Morales & Carlo 2006). Plant dispersal mechanisms or dispersal modes (the movement or transport of seeds away from the parent plant) could also be considered as a key factor in conservation biology and restoration management (Strykstra et al. 2002, Navarro et al. 2009a, Jara-Guerrero et al. 2011). Seed size is an im-

portant ecological trait for seedling establishment, formation of a persistent seed bank, and dispersal. In addition, seed size variation between or within species has important ecological and evolutionary significance in plant dispersal (Westoby et al. 1992). Generally, large seeds increase the chance of seedling survival and establishment, while small seeds contribute more to forming seed bank (Thompson et al. 1993). Likewise, large seed tends to be desiccation-tolerant under climate constraints in drylands (Pritchard et al. 2004). Seed size is often associated with growth form (Mazer 1989, Jurado et al. 1991, Lord et al. 1997), and dispersal mode (Ellner & Shmida 1981, Jurado et al. 1991, Navarro

et al. 2009a, 2009b). For example, large-seeded species are more likely to be animal dispersed, while small-seeded species are more likely to have unassisted seed dispersal (Leishman et al. 1995, Jurado et al. 2001, Navarro et al. 2009a).

The 'dispersal spectrum' is the frequency distribution of dispersal modes in a particular vegetation type (Howe & Smallwood 1982, Hughes et al. 1994). For several decades, researchers have been interested in studying of the dispersal spectra in different ecosystems (van der Pijl 1969, Frankie et al. 1974, Gentry 1982, Howe & Smallwood 1982, Navarro et al. 2006). In most studies, researchers are interested in assessing the relationship between the relative presence of dispersal modes in a particular site and the prevailing environmental conditions, such as temperature, precipitation, soil nutrient status or canopy structure (Willson et al. 1990, Bullcock 1995).

Anthropogenic disturbance has negative effects on forests and the activity of animal dispersers (Daniels et al. 1995). The dominance of species with structures that facilitate spatial dispersal by abiotic vectors (e.g. wind) tends to increase with growing disturbances (Ganeshiah et al. 1998, Nama & Choudhary 2013). In addition, it has been commonly reported that long-distance seed dispersal is less frequent in arid and semi-arid habitats than in mesic habitats and traits constraining seed dispersal are common in arid and semiarid floras (van der Pijl 1972, Ellner & Shmida 1981, van Rheede van Oudtshoorn & van Rooyen 1999, Navarro et al. 2009b). In this way, restrictions to seed dispersal have been widely used to explain the origin and maintenance of patches in arid vegetation (Kefi et al. 2008).

Seed size is correlated with flowering time (Mazer 1989, Navarro et al. 2009b) and consequently, with dispersal phenology (Navarro et al. 2009b). In hyper-arid hot deserts, phenological events are mainly related to the amount and time of annual rainfall and soil moisture condition (El-Keblawy et al. 2015a). The earlier flowering allows for a longer development time of seeds, which would promote larger seeds (Mazer 1990). Conversely, the later flowering gives a good chance for using more resources (moisture conditions) for seed development, but shorter time available for seed maturation and dispersal (Roux et al. 2006).

To our knowledge, no studies exist that assess dispersal traits and dispersal phenology in the Arabian desert. This kind of studies is particularly important for comparative ecological studies and for developing scientific conservation initiatives (Finckh 2006). We expect that dispersal spectrum could be similar to those recorded in other arid floras with the particularity of the presence of Afro-Arabian floristic elements. We also expect variation of the dispersal traits in the different studied habitats. The aims of this study are to examine the variation of diaspore size (seed and fruit length) among: (1) growth forms, (1) absence/presence structures facilitating long distance dispersal (spatial dispersal) (3) dispersal modes (4) APG IV phylogenetic taxonomic groups (5) phytogeography and (6) dispersal phenology in different habitat studied from the United Arab Emirates.

MATERIAL AND METHODS

Study area

The United Arab Emirates (UAE) are located in the south-eastern part of the Arabian Peninsula, between latitudes 22°40' and 26°00' North and longitudes 51°00' and 56°00' East, covering a total surface of 83 600 km². The UAE has a hyper-arid hot climate. The annual average temperature is approximately 27°C and humidity 45%. There are two main seasons; a rainy season with mild temperatures from November to March, with a mean temperature around 20°C and a dry hot season from April to October, with a mean temperature range between 35 and 40°C that can reach 47°C and humidity levels reaching more than 90%. The average amount of annual rainfall is around 110 mm with extreme variability in space and time and most of the rainfall occurring from January to April when temperatures are lowest (Böer 1997, UAE Ministry of Energy 2006, 2012, Sherif et al. 2009, UAE Ministry of Environment and Water 2015).

Our study is focused in inland forest and shrubland vegetation. Five different habitats were selected for this study: salt flats, gravel plains, sand sheets, mountains and high mountains (Jongbloed 2003, El-Keblawy et al. 2005, Karim & Fawzi 2007). The sites were selected to cover the main geomorphologic conditions characterizing the UAE (Böer & Gliddon 1997, Jongbloed 2003). Salt flats ("sabkha") separate the inland sandy areas and low Arabian Gulf coast. The salt flats region is dominated by *Zygophyllum qatarense* and *Salsola imbricata* with some frequent species such as *Heliotropium kotschyi*, *Fagonia ovalifolia*, *Arthrocnemum macrostachyum*, *Suaeda vermiculata*, *Haloepelis perfoliata* and *Anabasis setifera*. The gravel plains habitats are characterized by coarse sand and small rocky soils generally are dominated by *Acacia tortilis* mixed sometimes with *Prosopis cineraria*, cultivated palms (*Phoenix dactylifera*) and *Calotropis procera*. Most of the land surface of the UAE desert is covered with sand, which consists of a mixture of low dunes, high dunes and intervening sand flats. Sand sheets are dominated by *Cyperus conglomeratus*, *Tribulus omanense* and *Zygophyllum qatarense*. In the central desert, which is dominated by low sand dunes, the water table is deep and abounds in *Haloxyton salicornicum*, graminoids and some seasonal herbaceous plants such as *Stipagrostis plumosa*, *Cleome amblyocarpa* and *Eremobium aegyptiacum*. East of the Dubai region, the sand sheets abound in *Leptadenia pyrotechnica*, *Calligonum comosum* and *Calotropis procera*.

The mountain sites correspond to the Hajar Mountains series that extend from the UAE to the neighbouring Oman. Their elevations can reach more than 1000 m a.s.l. The common shrubby species in the mountains is *Euphorbia larica*. In the running wadis, trees such as *Prosopis cineraria* and *Ficus cordata* are dominant. On rocky hillsides (mountain), *Moringa peregrina* grows in addition to other graminoids and annuals (e.g. *Cymbopogon commutatus*, *Launaea spinosa*, *Filago desertorum* and *Reichardia tingitana*).

The high mountain habitats correspond to the North Mountains and are geologically distinct from the Hajar Mountains. They are sedimentary rocks, mostly carbonate with a peak at 2000 m a.s.l. *Ficus johannis* grow in these mountains, while

the high plateaux are covered with bushes (e.g. *Seriphidium herba-alba*). Some annual species, such as *Campanula erinus* and *Pentanema divaricata* grow in silt among the rocks.

Species selection

Field sampling and phenological observations were carried out monthly between May 2014 and October 2016. The selected species represent a cross-section of the flora of the arid/hyper-arid hot desert with xeric shrubland vegetation; importance was given to cover the most common and some rare species that characterize the vegetation (Jongbloed 2003, El-Keblawy et al. 2005, Karim & Fawzi 2007).

We selected 30 sampling points (quadrates) per studied habitat which represent a total of 150 quadrates (fig. 1, electronic appendix 1). The quadrat size was 200 m², in each quadrat the species dominance had been previously assessed with the relative importance values in which the abundance of the species has been estimated according to the Braun-Blanquet scale (Braun-Blanquet 1928). We discarded all the species that were present in less than 10% of all the relevés available. The selected dominant species probably represent

c. 80% of the total cover in the five studied sites. Voucher specimens of the most studied species were kept in the Sharjah Seed Bank and Herbarium (Sharjah Research Academy). Botanical nomenclature follows The International Plant Names Index (IPNI 2016). The family and class affiliation of each species used APG IV (Angiosperm Phylogeny Group 2016).

Dispersal, phenological and phytogeographical trait measurements

Seven easily measured dispersal traits were analysed: (1) dispersal mode which include anemo-meteochory, ombrohydrochory, semachory, ballistic and barochory, (2) diaspore size (diaspore length), (3) dispersal unit (fruit or seed) (3) presence of structures facilitating long-distance dispersal (4) diaspore appendages (5) diaspore colour, and (6) dispersal phenotype (electronic appendix 2).

Among dispersal traits, the dispersal mode and diaspore size (diaspore length) constitute the main regenerative traits according to Cornelissen et al. (2003) and Pérez-Harguindéguay et al. (2013). Dispersal modes follow van der Pijl (1982).

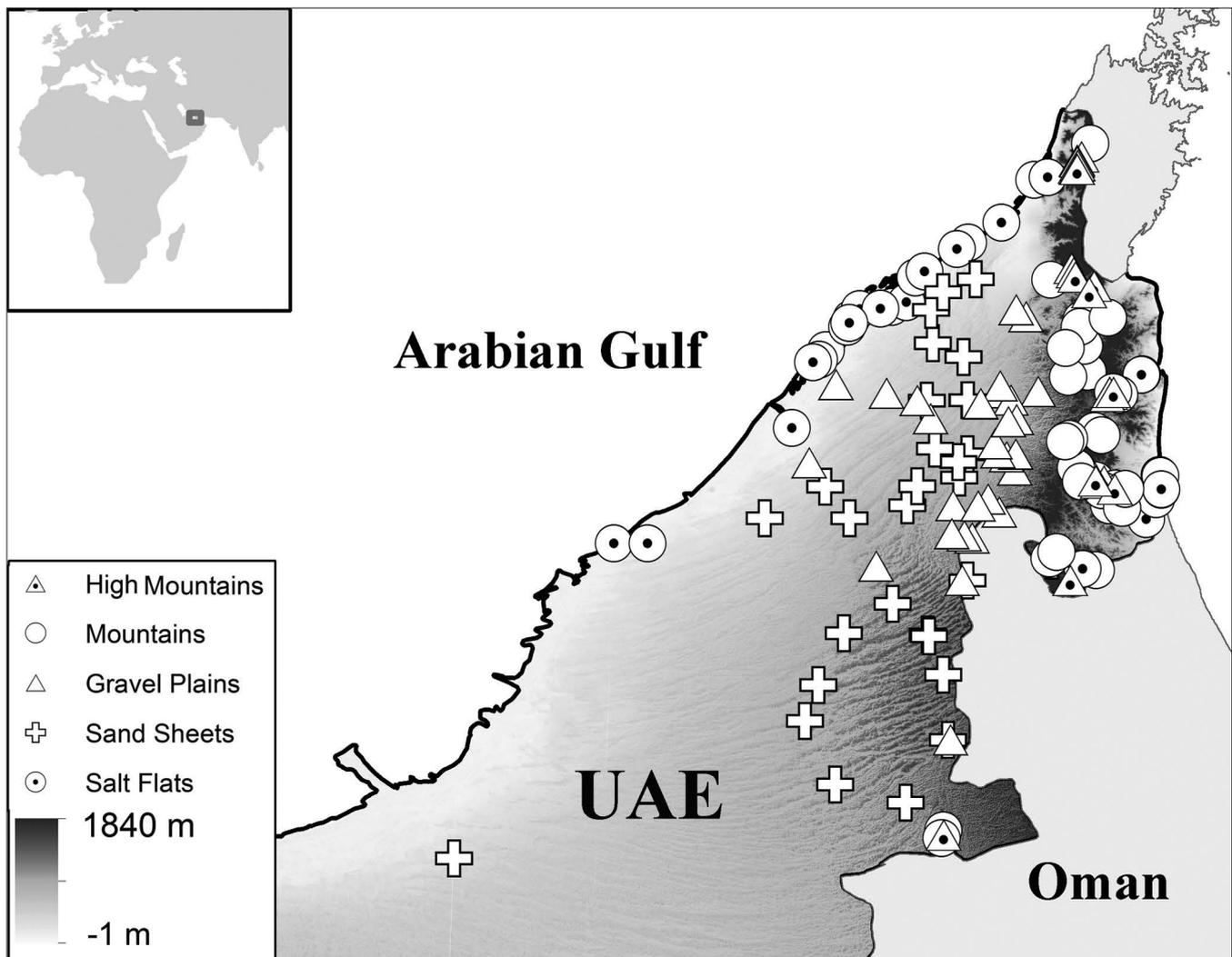


Figure 1 – Illustration map for the 150 sampled quadrates in the study area from the hyper-arid hot desert of United Arab Emirates.

Whenever a diaspore lent itself to more than one type of dispersal mode, the predominant form observed in more than 80% of sampling quadrates was generally used.

To measure diaspore size (diaspore length), diaspores were collected when ripe but before they started to fall off the plant. For each individual species, 100 diaspores were air-dried and their mean size was measured as the longest dimension (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013). The achenes of Asteraceae were measured with the pappus. Exceptionally, when they were not available in the necessary quantities, the data were completed based on Flora databases (e.g. Flora of Pakistan 2016, <http://www.tropicos.org/Project/Pakistan>) and references (Miller & Cope 1996, Jongbloed 2003, Boulos 2009).

The term diaspore was used to name the dispersal unit (Weiher et al. 1999). We scored whether species had diaspores equipped with structures that facilitate spatial dispersal, such as pappi, barbs or wings for dispersal by abiotic vectors (e.g. wind) or fleshy fruits to dispersal by biotic vectors (e.g. vertebrates) (Ellner & Shmida 1981, Venable & Levin 1985, Cain et al. 2000). Species were considered as having restricted dispersal if diaspores lacked such dispersal-enhancing characters (Willson 1993). Anemo-meteochoric species have structures facilitating long-distance dispersal by abiotic vectors (e.g. wind); barochory species have fleshy fruits or pods with nutrients structures facilitating long-distance dispersal by biotic vectors (e.g. vertebrates); ombrohydrochory, semachory and ballistic species lack structures facilitating long-distance dispersal. Diaspore appendage type were determined following Thomson et al. (2018) and based on the field observations. The colour categories follow (Wheelwright & Janson 1985); black (including dark red), red (including pink), yellow, orange, brown, grey, green, white and blue (including purple).

To establish dispersal phenology (rainy or dry season), phenological surveys were performed for at least 2.5 years.

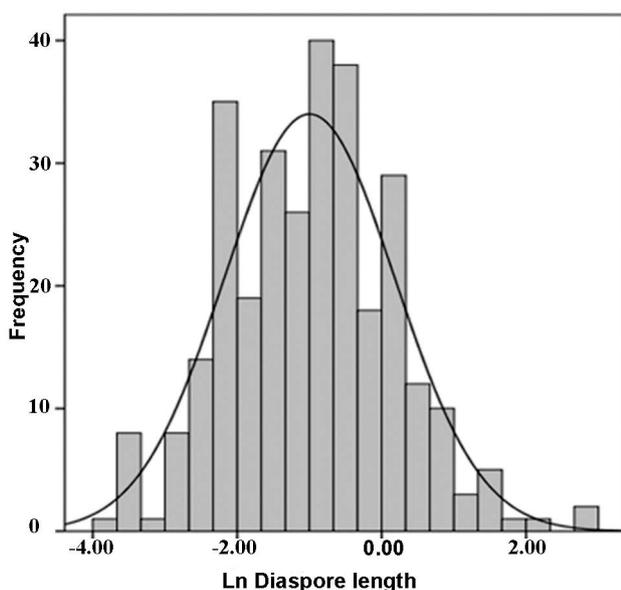


Figure 2 – Frequency of seed length (Ln) of studied species in the hyper-arid hot desert of United Arab Emirates.

In each year, the units of vegetation from each site were observed 10–12 times at approximately 30–45-day intervals. The onset of dispersal (the beginning of dispersal time) was described (electronic appendix 2).

Species were classified in ten growth forms following Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013) (electronic appendix 2).

Species were classified on the basis of their biogeographical distribution in desert regions of the world (Good 1964, Evenary et al. 1985). The major phytogeographical regions were: the central Australian region, the western and central Asian region (Irano-Turanian region, Eig 1931, 1932, Zohary 1973) and the African-Indian region (Saharo-Sindian region, Eig 1931, 1932), where our study area is located. Following these authors nine phytogeographical regions were recognized in order to establish relationships between dispersal traits and species biogeography. Species, family, habitats, dispersal traits, phytogeography and dispersal phenology of the studied species are presented in the electronic appendix 2.

Statistical analyses

One-way analysis of variance (ANOVA), followed by the post hoc comparisons (Tukey HSD test), was used to test the significance of differences ($p < 0.01$) of log diaspore size among APG IV groups and dispersal traits. Categories with less than seven species were excluded from the analyses. The association between nominal traits was determined with the Pearson χ^2 test-statistic. All statistical analyses were performed with SPSS 14 and SYSTAT 13.

RESULTS

A total of 302 species, belonging to 51 families and 192 genera, were studied (electronic appendix 2). Fabaceae (12.6% of total species), Asteraceae (9.9% of total species), Poaceae (9.6% of total species) and Amaranthaceae (7.6% of total species) were the richest families. Fabaceae species were recorded in all habitats. Asteraceae were absent in salt flats and Poaceae and Amaranthaceae were absent from high mountains.

Eight phylogenetic APG IV groups were represented: Fabids (67 species, 22.2%), Basal Asterids (20.5%), Lamiids (17.5%), Malvids (14.6%), Commelinids (11.6%), Campanulids (11.3%), Monocots (1.7%) and Basal Rosids (0.7%). 82 species (27.2%) were exclusively Saharo-Arabian (SA) and Sudano-Deccanian (SD) species and were present in all habitats (electronic appendix 2).

A percentage of 53.6% of the studied species were woody species, 34.8% herbaceous and 11.6% graminoids species. The dominant growth form was dwarf shrubs (41.1%) followed by semi-basal herbs (21.9%) and tussocks (11.6%). The dispersal phenology of studied species was in the dry season (from April to October, 63.9% of total species) followed by the rainy season (from November to March, 32.1% of total species), and throughout the year (4% of total species) (electronic appendix 2).

The range of diaspore size (diaspore length) spanned six orders of magnitude from 10^{-4} to 10^2 (fig. 2). The diaspore

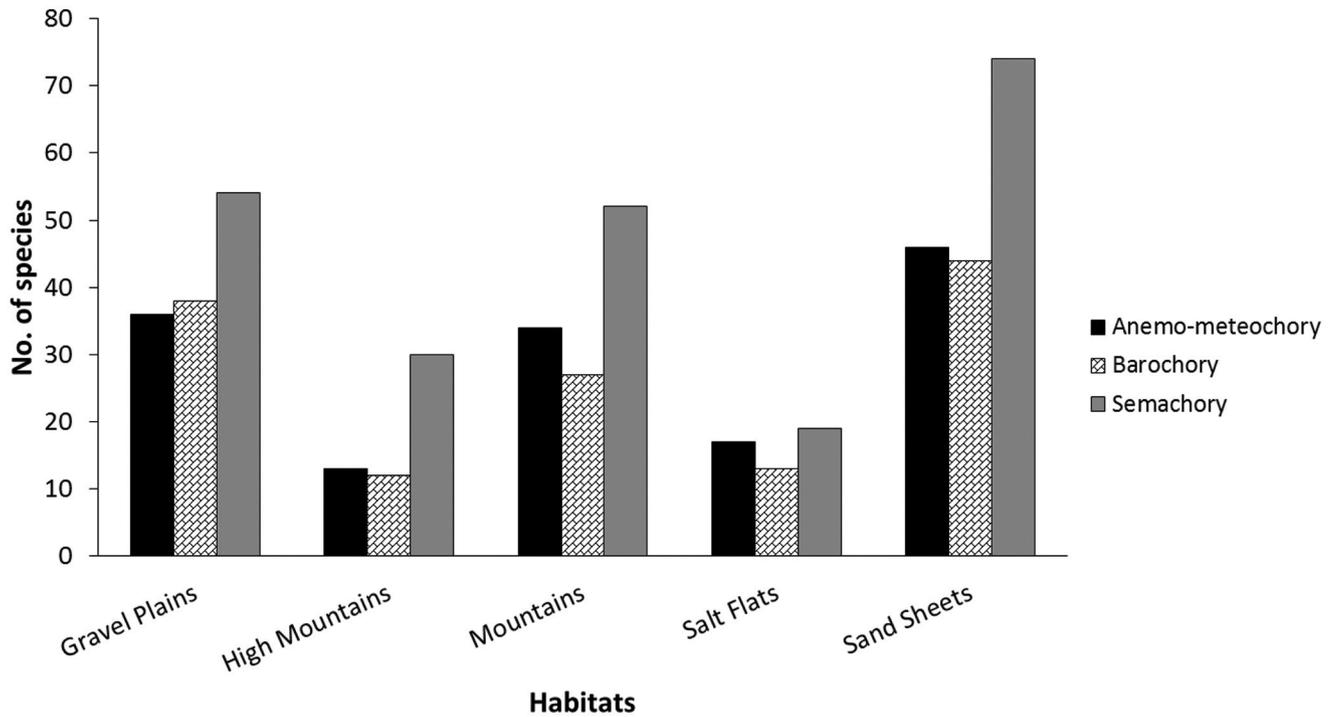


Figure 3 – Frequency distribution of dispersal modes among species in the five studied habitats from the hyper-arid hot desert of United Arab Emirates.

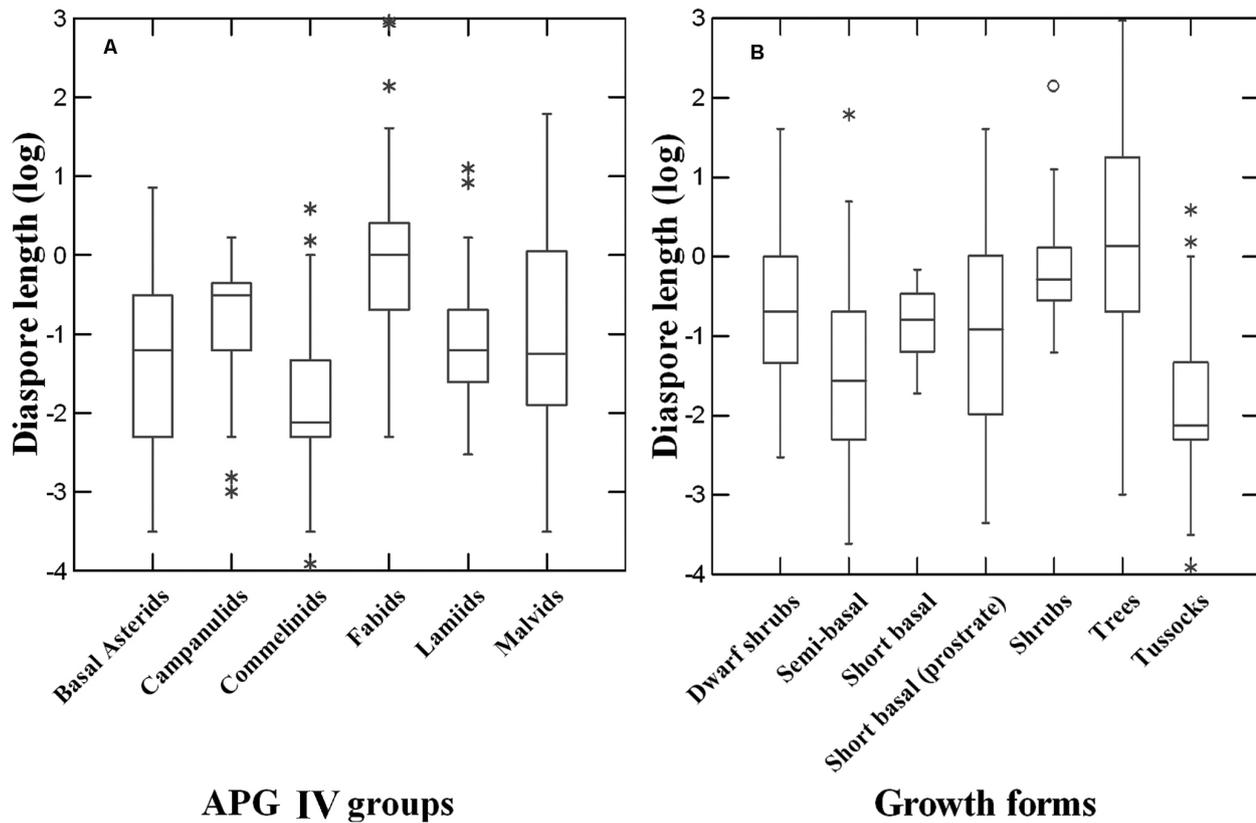


Figure 4 – Diaspore length variation among A, APG IV phylogenetic taxonomic groups and B, growth forms of studied species from the hyper-arid hot desert of United Arab Emirates. (Cornelissen et al. 2003 and Pérez-Harguindeguy et al. 2013).

Table 1 – Mean and standard error (SE) of nine traits studied in the 302 plant species from the hyper-arid hot desert of United Arab Emirates.

Nine traits are: APG IV, growth forms, absence/presence structures facilitating long distance dispersal, dispersal mode, absence/presence of appendage type, diaspore colour, phytogeographical regions, habitats, dispersal phenology.

Trait	Category	Mean±SE	Trait	Category	Mean±SE
APG IV	Basal Asterids	0.42±0.06	Diaspore colour	Black	0.20±0.02
	Campanulids	0.55±0.05		Brown	0.80±0.09
	Commelinids	0.30±0.08		Green	0.67±0.09
	Fabids	1.80±0.41		Red	0.65±0.12
	Lamiids	0.45±0.07		White	0.73±0.21
	Malvids	0.87±0.20		Yellow	2.74±1.34
Growth forms	Dwarf shrubs	0.74±0.07	Phytogeographical regions	Cosm	0.40±0.17
	Semi-basal	0.41±0.10		SA	0.35±0.06
	Short basal (prostrate)	0.77±0.20		SA, IT	0.67±0.09
	Trees	3.85±1.76		SA, IT, Med	0.43±0.07
	Shrubs	1.40±0.43		SA, IT, SD, Med	0.68±0.14
	Short basal	0.47±0.06		SA, Med	0.51±0.08
	Tussocks	0.30±0.08		SA, SD	1.24±0.27
Absence/presence structures facilitating long distance dispersal	Absence (restricted dispersal)	0.47±0.06		SA, SD, IT	1.27±0.71
	Presence (dispersal by abiotic vectors)	0.68±0.07		SA, SD, Med	0.65±0.22
	Presence (dispersal by biotic vectors)	2.52±0.71	Habitats	Mountains	0.64±0.08
Dispersal mode	Semachory	0.37±0.04		Gravel Plains	0.86±0.17
	Anemo-meteochory	0.69±0.07		Sand Sheets	0.96±0.17
	Barochory	1.77±0.39		Salt Flats	0.83±0.39
Absence/presence of appendage type	Absence	0.85±0.15		High Mountains	0.65±0.10
	Pappus	0.57±0.05	Dispersal phenology	Dry	0.78±0.12
	Spine	0.60±0.09		Rainy	0.61±0.09
	Wings	0.68±0.08		All the year	2.34±1.58

size ranged from 0.02 cm in *Sporobolus spicatus* (Poaceae) to 19.5 cm in *Prosopis juliflora* (Fabaceae).

Dispersal spectrum

Fruits (69.7%) were the dominant dispersal unit. Species lacking structures for long-distance dispersal (restricted dispersal) were more represented (58.6%), compared to species with developed structures for dispersal by abiotic vectors (29.1%) or by biotic vectors (12.3%). The main dispersal mode was semachory (43.7%), followed by anemo-meteochory (28.8%), and barochory (23.8%).

Semachory was predominant in all studied habitats followed by anemo-meteochory and semachory, respectively (fig. 3). Ballistic species were absent in salt flats, ombrohydrochories were absent in high mountains and zoochoric

species were represented only in mountains, sand sheets and gravel plains.

The predominant diaspore colour was brown (51.0%), followed by black (17.5%), green (11.9%), white (7.6%), yellow (6.3%), and reddish (4%).

A total of 60% of studied species lacked diaspore appendages. 48% of anemo-meteochoric species had winged appendages and 46.6% of them pappus. The anemo-meteochoric species with wings were dominant in sand sheets (33.3%) while species with pappus were dominant in gravel plains, mountains and sand sheets (27.6% in each habitat).

Variation of diaspore size (diaspore length) among APG IV groups and dispersal traits

The diaspore length differed significantly among the different APG IV phylogenetic taxonomic groups (F (5, 289)

= 17.052; $p \leq 0.001$). The post hoc comparisons (Tukey HSD test) shows that the mean of diaspore length of Fabids (1.80 ± 0.41 cm) was significantly longer than Malvids (0.87 ± 0.20 cm), Campanulids (0.55 ± 0.05 cm), Lamiids (0.45 ± 0.07 cm), Basal Asterids (0.42 ± 0.06 cm) and Commelinids (0.30 ± 0.08 cm). Fabids and Malvids had the largest diaspores (e.g. *Prosopis juliflora*, 19.5 cm and *Cleome amblyocarpa*, 6.0 cm), while Commelinids had the smallest diaspores (e.g. *Sporobolus spicatus*, 0.02 cm) (fig. 4A, table 1).

Diaspore length differed significantly among growth forms ($F(6, 289) = 13.012$; $p \leq 0.001$). The post hoc comparisons (Tukey HSD test) shows that the mean of diaspore length of tussocks (0.30 ± 0.08 cm) was it was significantly lower that dwarf shrubs (0.74 ± 0.07 cm), short basal (prostrate) (0.77 ± 0.20 cm), shrubs (1.40 ± 0.43 cm) and trees (3.85 ± 1.76 cm). This means, trees had the largest diaspore size (e.g. *Prosopis juliflora*, 19.5 cm), while tussocks had the smallest sizes (e.g. *Sporobolus spicatus*, 0.02 cm and *Cenchrus ciliaris*, 0.03 cm) (fig. 4B, table 1).

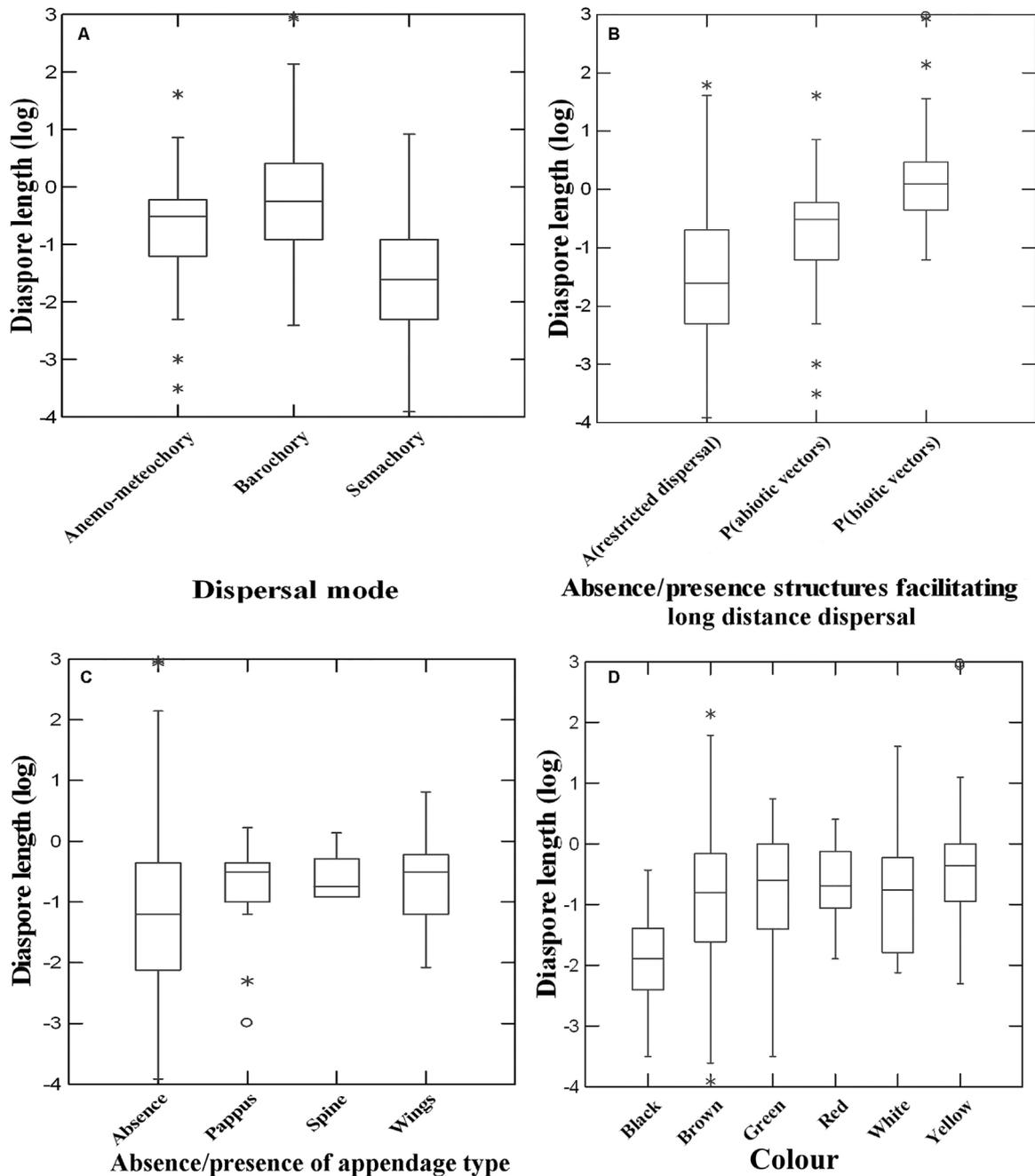
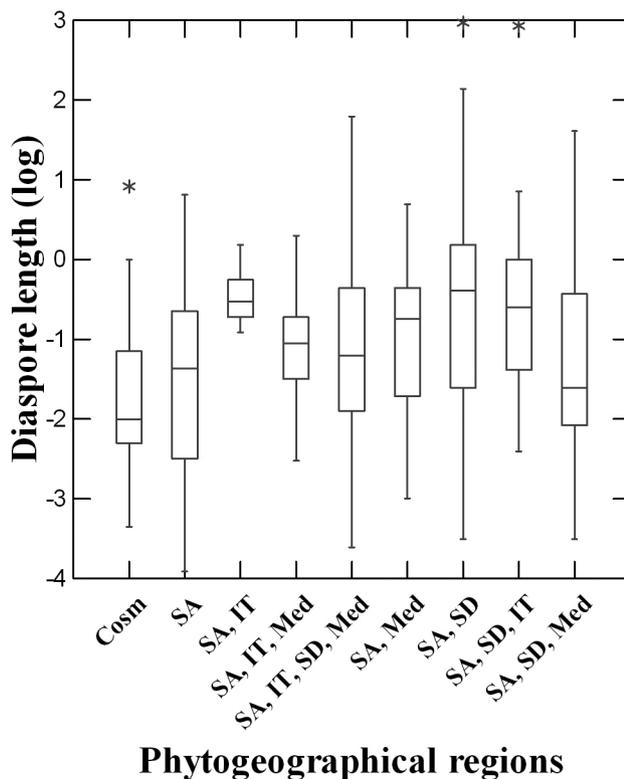


Figure 5 – Diaspore length variation among dispersal traits in the studied species from the hyper-arid hot desert of United Arab Emirates; A, dispersal mode; B, absence/presence structures facilitating long distance dispersal; C, absence/presence of appendage type; D, diaspore colour.

Diaspore length differed significantly among the different dispersal mode ($F(2, 288) = 39.720; p \leq 0.001$). The post hoc comparisons (Tukey HSD test) shows that the mean of diaspore length of semachoric species (0.37 ± 0.04 cm) was significantly lower than the anemo-meteochoric (0.69 ± 0.07 cm) and barochoric species (1.77 ± 0.39 cm). Barochoric species (e.g. *Prosopis cineraria*, 18.8 cm) were the largest, while semachoric species (e.g. *Tillaea alata*, 0.027 cm) were the smallest (fig. 5A, table 1).

Diaspore length differed significantly according to the presence/absence of developed structures for long-distance dispersal ($F(2, 299) = 42.590; p \leq 0.001$). The post hoc comparisons (Tukey HSD test) shows that the mean of diaspore length of species dispersed by developed biotic vectors (2.52 ± 0.71 cm) was significantly longer from the species dispersed by developed abiotic vectors (0.68 ± 0.07 cm) and species with restricted spatial dispersal (0.47 ± 0.06 cm). Species dispersed by biotic vectors (e.g. *Prosopis cineraria*, 18.8 cm and *Calligonum comosum*, 1.2 cm) had the larger diaspore size than those dispersed by abiotic vectors and species who lack structures facilitating long-distance dispersal (e.g. *Reseda aucheri*, 0.08 cm, fig. 5B, table 1).

Diaspore length differed significantly according absence or presence or appendages ($F(3, 271) = 2.956; p \leq 0.05$).



Phylogeographical regions

Figure 6 – Diaspore length variation among phylogeographical regions of studied species from the hyper-arid hot desert of United Arab Emirates. Phylogeographical regions: AU, Australian; Cosm, Cosmopolitan; IT, Irano-Turanian; Med, Mediterranean. NAM, North American; SAF, Southern African; SAM, South American; SA, Saharo-Arabian; SD, Sudano-Deccanian.

Species lacking appendages facilitating long-distance dispersal have longer diaspores (fig. 5C, table 1).

Diaspore length differed significantly according to diaspore colour ($F(5, 289) = 9.408; p \leq 0.001$). The post hoc comparisons (Tukey HSD test) shows that the mean diaspore length of black diaspores (0.20 ± 0.02 cm) was significantly lower than the red (0.65 ± 0.12 cm), green (0.67 ± 0.09 cm), white (0.73 ± 0.21 cm), brown (0.80 ± 0.09 cm) and yellow diaspores (2.74 ± 1.34 cm). Species with green and yellow diaspores (e.g. *Prosopis juliflora*, 19.5 cm and *Rhynchosia schimperi*, 2.1 cm, respectively) were the largest, while black diaspores (e.g. *Polycarpha repens*, 0.03 cm) were the smallest (fig. 5D, table 1).

Diaspore length differed significantly among the different phytogeographical regions ($F(8, 293) = 3.672; p \leq 0.001$). The post hoc comparison (Tukey HSD test) shows that the mean of diaspore length of species belongs to Saharo-Arabian and a Sudano-Deccanian region (1.24 ± 0.27 cm) was significantly bigger than to Cosmopolitan (0.40 ± 0.17 cm) and Saharo-Arabian species (0.35 ± 0.06 cm). Saharo-Arabian and Sudano-Deccanian species (e.g. *Acacia ehrenbergiana*, 8.5 cm) had the largest seeds, while Saharo-Arabian and Cosmopolitan species had the smallest (e.g. *Limeum indicum*, 0.02 cm, fig. 6, table 1).

No significant difference was observed in diaspore length among habitat types ($F(4, 527) = 0.581; p \leq 0.676$) or among dispersal phenology ($F(2, 299) = 1.233; p \leq 0.293$).

Relationships between dispersal modes, APG IV phylogenetic groups, growth forms and dispersal phenology

There were significant relationships between APG IV phylogenetic taxonomic groups and dispersal modes ($\chi^2 = 119.354; df = 10; p \leq 0.001$, fig. 7A). Barochory was more common in Fabids and absent in Campanulids (fig. 7A). In addition, anemo-meteochory was over-represented in Basal Asterids and Campanulids (fig. 7A). Semachory was predominant in Lamiids, Commelinids and Malvids (fig. 7A).

Significant relationships were detected between dispersal modes and growth forms ($\chi^2 = 79.427; df = 12; p \leq 0.001$, fig. 7B). Semachory was more represented in herbaceous species, such as semi-basal, prostrate herbs and tussock graminoids. Barochory was predominant in trees and shrubs (fig. 7B). Anemo-meteochory was over-represented only in dwarf shrubs (fig. 7B).

Significant relationships were detected between dispersal modes and dispersal phenology ($\chi^2 = 15.506; df = 4; p \leq 0.01$). Dispersal was concentrated in dry season (fig. 8, electronic appendix 2).

Relationships between presence/absence of developed structures facilitating long-distance dispersal, APG IV phylogenetic groups, growth forms, phylogeography and dispersal phenology

There were significant relationships between APG IV phylogenetic taxonomic groups and the presence/absence of developed structures for long-distance dispersal ($\chi^2 = 119.99; df = 10; p < 0.001$, fig. 9A). Absence of structures for long-

distance dispersal was the most common in all phylogenetic taxonomic groups except for Campanulids, in which developed structures for dispersal by abiotic vectors was over-represented (fig. 9A). Developed dispersal by biotic vectors was present only in Lamids, Malvids and Fabids (fig. 9A).

Significant relationships were detected between the presence/absence of developed structures for long-distance dispersal and growth forms ($\chi^2 = 92.054$; $df = 12$; $p \leq 0.001$, fig. 9B). Absence of structures for long-distance dispersal was overrepresented in herbaceous species and dwarf shrubs (fig. 9B). Presence of structures for long-distance dispersal by biotic vectors was mainly prevalent in trees (fig. 9B), while presence of structures for long-distance dispersal by abiotic vectors was over represented only in shrubs (fig. 9B). Significant relationships were detected between the presence/absence of developed structures for long-distance dispersal and species phylogeographical distribution ($\chi^2 = 48.268$; $df = 16$; $p \leq 0.001$, fig. 10). Developed structures for dispersal by

biotic vectors were mainly associated with Sudano-Decanian species (fig. 10), which are species forming part of African vegetation in the study area. Saharo-Arabian species were exclusively restricted dispersal and they were dominant species in all regions except in the Saharo-Arabian and Irano-Turanian region.

Significant relationships were detected between the presence/absence of developed structures for long-distance dispersal and dispersal phenology ($\chi^2 = 15.644$; $df = 4$; $p \leq 0.004$). A total of 63.6% of the species with developed structures for long-distance dispersal dispersed in the dry season from May to October (fig. 11).

DISCUSSION

The range of seed size variation in the studied species in the hot UAE deserts coincides with that found in other arid and semi-arid ecosystems (Jurado et al. 1991, 2001, Leish-

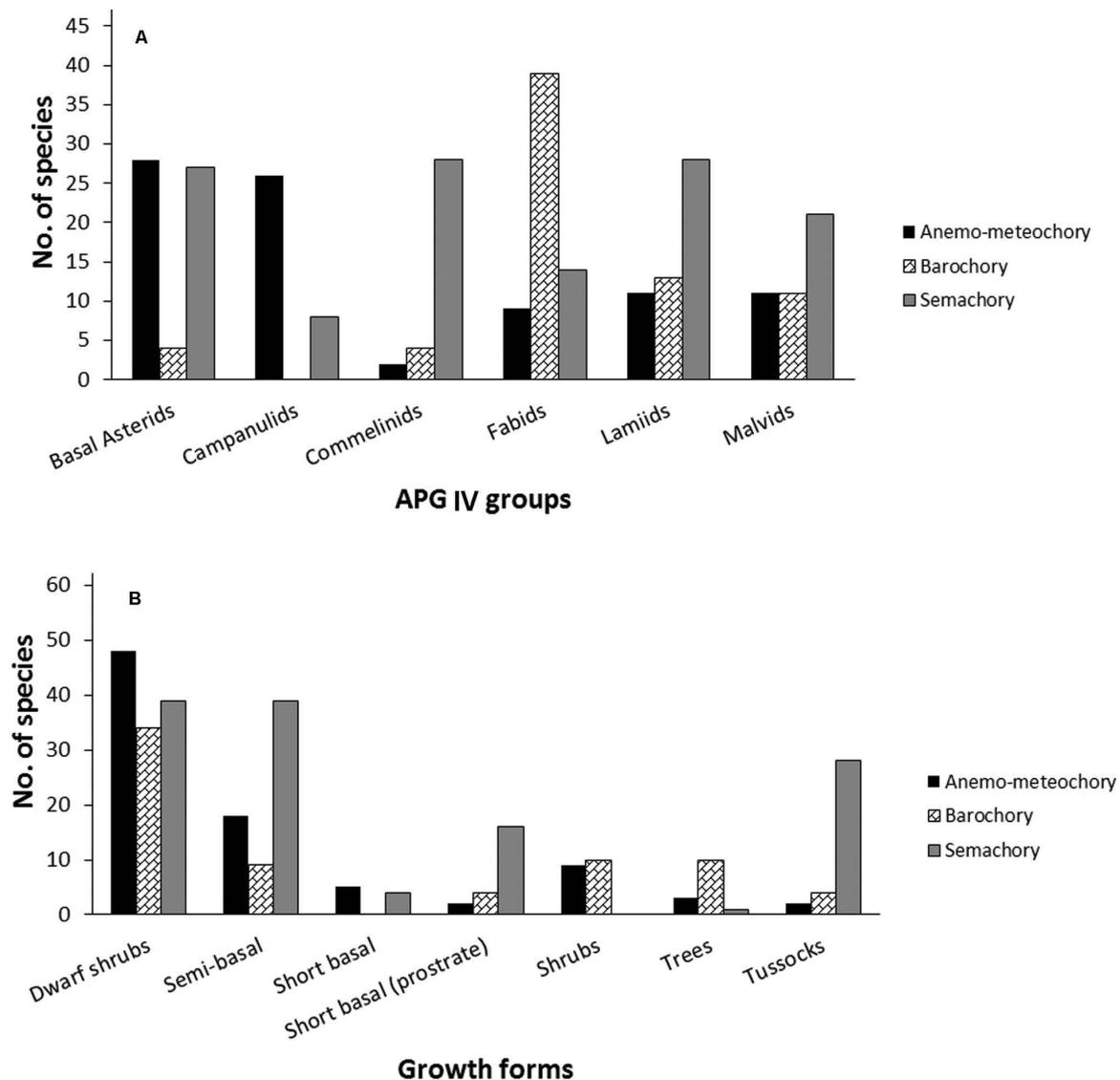


Figure 7 – Frequency distribution of dispersal modes among APG IV phylogenetic groups and growth forms of studied species from the hyper-arid hot desert of United Arab Emirates.

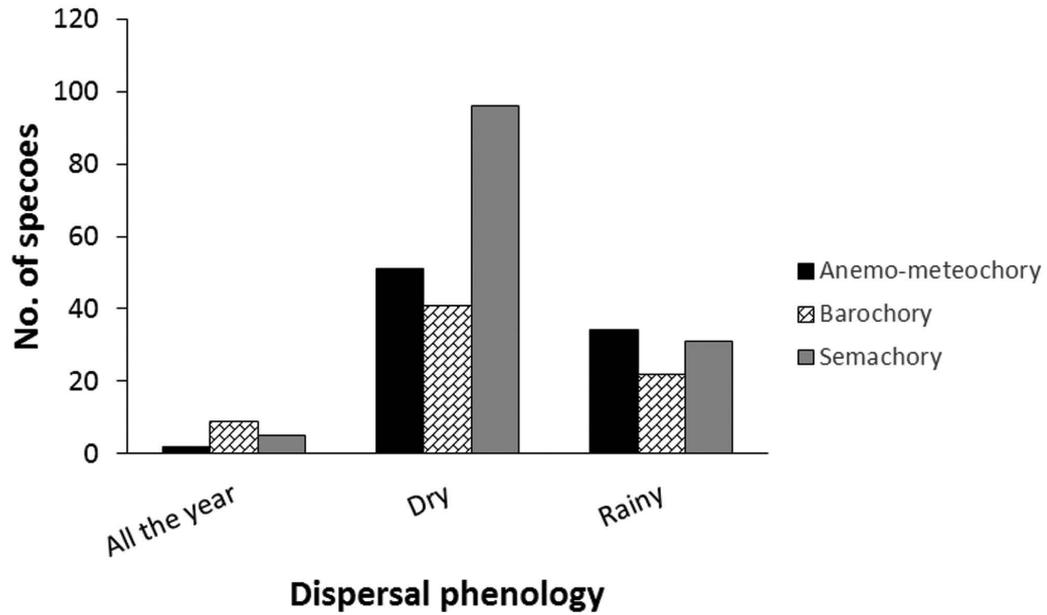


Figure 8 – Frequency distribution of dispersal modes among dispersal phenology of studied species from the hyper-arid hot desert of United Arab Emirates.

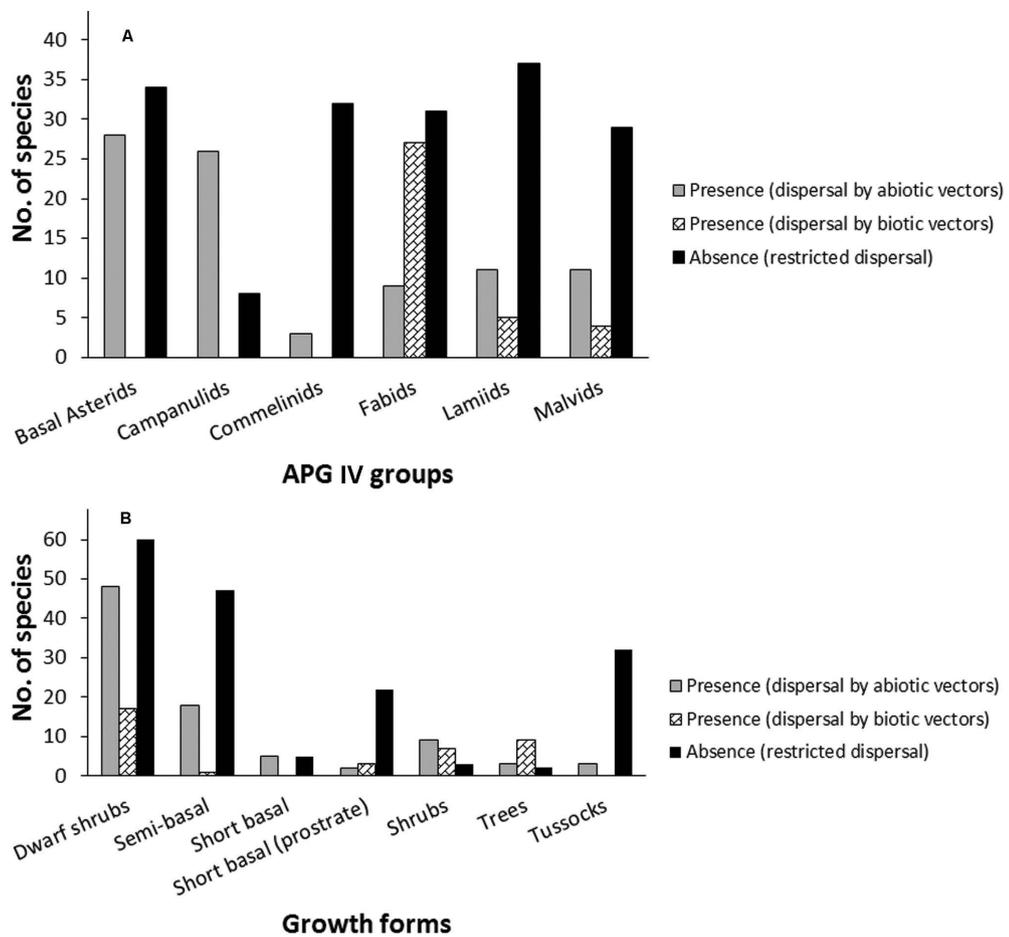


Figure 9 – Frequency distribution of absence/presence structures facilitating long distance dispersal among APG IV phylogenetic groups and growth forms of studied species from the hyper-arid hot desert of United Arab Emirates.

man et al. 2000, Navarro et al. 2006, 2009a). However, in the UAE deserts, there were no very small ($\log, 10^{-4}$) or very large diaspores ($\log, 10^2$). Harel et al. (2011) reported that seed size significantly decreased with increasing aridity and rainfall variability in seven out of fifteen sites in the hot Negev Desert. Our results are in agreement with previous studies that indicate that the largest diaspores were represented in the Fabaceae family while the smallest diaspores were found in Poaceae (Mazer 1989, Liu et al. 2014). The advantage of small seeds is a lower risk of being eaten by predators (Hulme 1994, van Rheede van Oudtshoorn & van Rooyen 1999); their small size enables them to fall into soil cracks and consequently avoid detection by predators (Gutterman 2002). This indicates that small seeds could form a long-lived seed bank in the desert, which ensures species survival under the heterogeneous and unpredictable desert conditions. However, the small reserves in the small seeds would not help them to emerge from deep soil unless some kind of disturbance happens (El-Keblawy et al. 2015b, El-Keblawy & Gairola 2017, El-Keblawy 2017). On the other hand, small seeds tend to be desiccation-sensitive seeds that germinate rapidly because delayed germination can induce seed death (Pritchard et al. 2004), as is the case of the ombro-hydrochoric species.

The seed dispersal spectrum of the studied hyper-arid hot desert in the UAE was characterized by the dominance of semachory (43.7%), followed by anemo-meteochory (28.8%) and barochory (23.8%). Nevertheless, semachory/barochory is the largest group (67.5%). Other species in the

Amaranthaceae, Zygophyllaceae, Brassicaceae and Poaceae families are semachores, just like other species in the Fabaceae and Zygophyllaceae families are barochores with larger seeds that can take full advantage of the favorable surrounding conditions and germinate fast and to high levels (Liu et al. 2014). About 68.5% of the semachoric species were herbaceous, which is consistent with other desert ecosystems (van Rheede van Oudtshoorn & van Rooyen 1999). Zoochory has been described as the most dominant mechanism (more than 80%) in humid and dry tropical forests (Fleming 1979, Gentry 1982), but its presence decreases in ecosystems with dryer climates (Gentry 1982). In temperate areas, barochoric species are significantly more frequent than anemometeochoic and zoochoric species (Leishman et al. 1995, Wang et al. 2009). However, semachoric species lacking long-dispersal structures, are more frequent in our study area helping the seeds to stay near the mother plants, which could be considered as “safe sites” for seedling establishment (van Rheede van Oudtshoorn & van Rooyen 1999, Rodriguez et al. 2017). Only three of the studied species were zoochoric (the epizoochoric *Tragus racemosus* and *Medicago* sp.). The low frequency of epizoochory could reflect the low presence of mammals in the harsh desert conditions.

Several studies have reported a relationship between dispersal syndromes and plant growth form (van der Pijl 1969, Frantzen & Bouman 1989, Willson et al. 1990, Griz & Machado 2001, Navarro et al. 2009a, 2009b). Anemo-meteochory was predominant in dwarf shrubs and shrubs in the tropical dry forest (Griz & Machado 2001) and in the Medi-

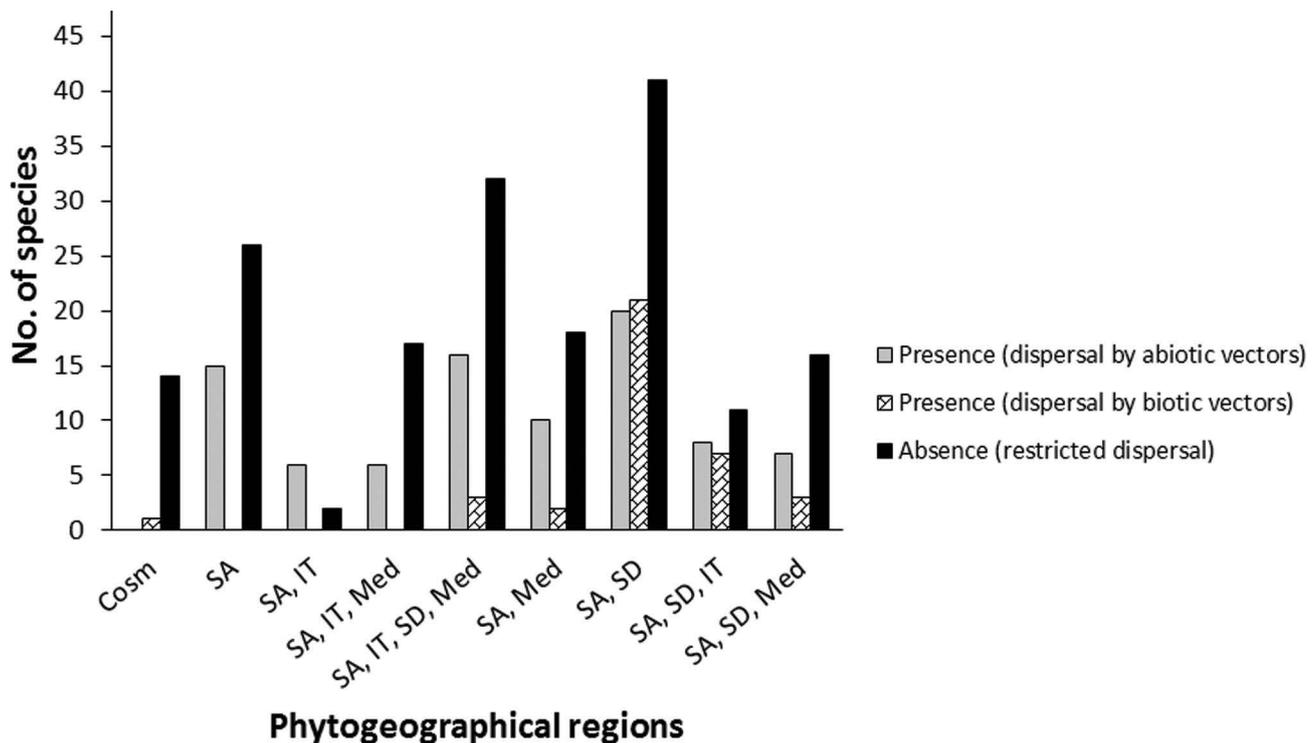


Figure 10 – Frequency distribution of absence/presence structures facilitating long distance dispersal among phytogeographical regions of studied species from the hyper-arid hot desert of United Arab Emirates. Phytogeographical regions: AU, Australian; Cosm, Cosmopolitan; IT, Irano-Turanian; Med, Mediterranean. NAM, North American; SAF, Southern African; SAM, South American; SA, Saharo-Arabian; SD, Sudano-Deccanian.

terranean dry shrublands (Navarro et al. 2009a). In our study, trees and large shrubs are barochoric species produce large fleshy fruits or pods with nutritive structures (e.g. *Acacia* sp., *Indigofera* sp., *Prosopis* sp. and *Ziziphus* sp.) dispersed secondarily by vertebrates (Jurado et al. 1991, 2001, Leishman & Westoby 1994). Westoby et al. (1992) have proposed that diaspore size tends to be associated with plant size and the longevity of trees and large shrubs of unfavorable habitats (Puigdefàbregas & Pugnaire 1999) with desiccation-tolerant seeds (Pritchard et al. 2004).

In the desert region, restricted spatial dispersal is more dominant than developed spatial dispersal and was more represented in herbaceous and graminoids than woody species (Ellner & Shmida 1981). These species can survive in situ, with regeneration and plant recovery in extreme and hard climatic conditions (Gutterman & Shem-Tov 1997, van Rheede van Oudtshoorn & van Rooyen 1999). The graminoids living preferably in the gravel plains and mountains having appendages which enable them to be effectively dispersed by the wind, pass through the cracks of the biological soil crusts, and settle down, such as *Stipa* sp., *Stipagrostis* sp. and *Aristida* sp., which could take a special way named “active drill” into soil cracks using mucrons (Schöning et al. 2004, García-Fayos et al. 2013). Brassicaceae, Lamiaceae and Scrophulariaceae herbaceous species are mainly restricted spatial-dispersal species with relatively small seeds, as found in other arid regions (Navarro et al. 2009a, 2009b). Efficient spatial dispersal is associated with the presence of morphological structures favors dispersal long-distance by the wind such as hairy capsules (e.g. *Aerva javanica*), winged calyx (e.g. *Astragalus squarrosus*), wings (e.g. *Tribulus* sp.) or pappus in the Asteraceae species.

Dispersal mechanisms can be associated with climatic factors (Gentry 1982, Wikander 1984, Griz & Machado

2001, Navarro et al. 2009a, Jara-Guerrero et al. 2011), and most probably with the temporal patterns of water availability. These factors have the largest impact on plant propagation in hyper-arid hot desert as in other hot dry regions (Griz & Machado 2001). In the savannas of West Africa, strong relationships were found between fruiting and soil moisture, which may reflect a selection of dispersal periods that maximizes seed dispersion and germination (Seghieri et al. 2009). In our study, 25.1% of species disperse in the rainy seasons and they are mainly Sudano-Decanian barochoric species (Afro-Arabian species) (electronic appendix 2), which form part of the savanna vegetation.

The results of our study showed that species dispersed by abiotic vectors (wind) have a dispersal peak in synchronization with the dry season, as found in other regions with climatic restrictions, such as Mediterranean (Navarro et al. 2009a, 2009b), desert (van Rooyen et al. 1990) and dry tropical regions (Machado et al. 1997, Griz & Machado 2001).

Continuous patterns of dispersal throughout the year were observed in some of the studied species. This indicates an important seed supply to occur in the ecosystems that are characterized by seasonal variation and where a rainfall could be expected at any time of the year (Machado et al. 1997). These species correspond to barochoric species with large fleshy fruits (e.g. *Ziziphus* sp., *Solanum* sp.) or pods with nutrient structures (e.g. *Senna italica*, *Indigofera* sp., *Tephrosia* sp.). Interestingly, species that can disperse throughout the year have lower dormancy and are able to germinate at a wider range of environmental conditions; consequently, they can contribute to seedling recruitment at any time of the year (El-Keblawy 2017).

To conclude, the observed patterns suggest that the seed dispersal spectrum of the hyper arid hot desert of UAE follows the general patterns of arid and desert ecosystems with

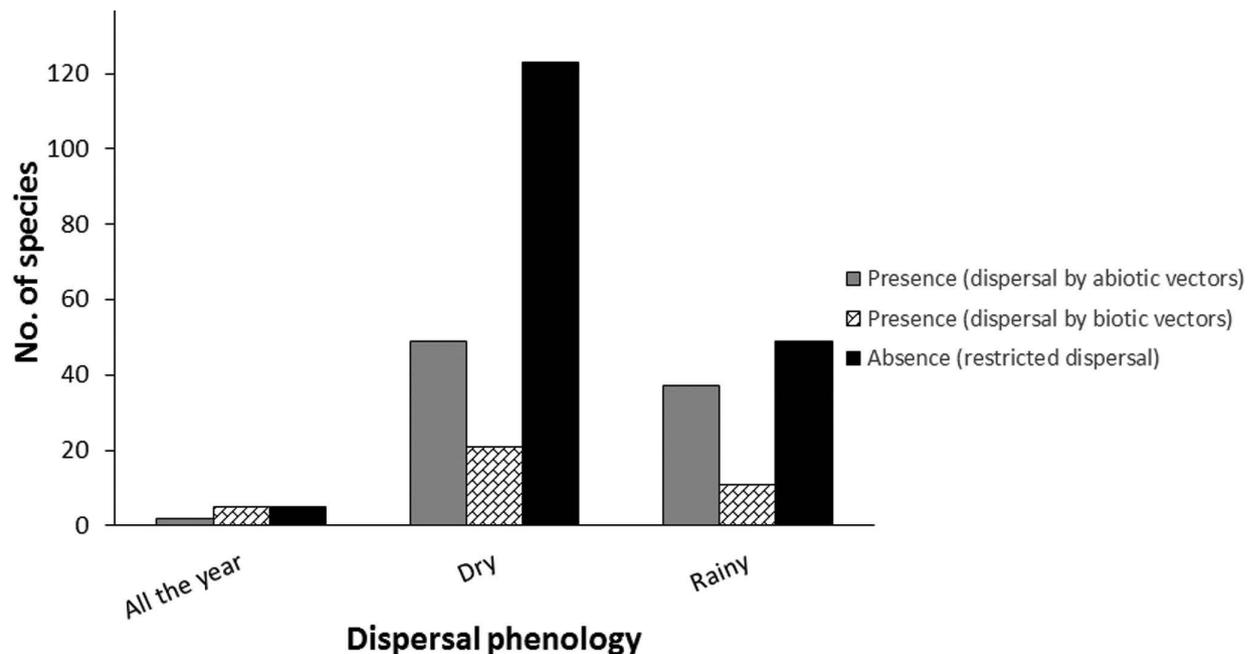


Figure 11 – Frequency distribution of absence/presence structures facilitating long distance dispersal among dispersal phenology of studied species from the hyper-arid hot desert of United Arab Emirates.

some particularities due to the UAE floristic richness explained by the presence of African floristic elements. Seed/fruit availability is limited by fruiting seasonality in altered habitats. In general, diaspore characteristics were closely related to phylogeny, dispersal modes and growth forms and these characteristics allowed the plants to adapt to extreme hot desert environments.

SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data Site (<https://www.ingentaconnect.com/content/botbel/plecevo/supp-data>) and consist of: (1) list of the habitats studied including the geographical references for the 150 sampled quadrates from the hyper-arid hot desert of the United Arab Emirates; and (2) the species, family, habitats, APG IV phylogenetic group, growth forms, phytogeography and dispersal traits of 302 species from hyper-arid hot desert of the United Arab Emirates.

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