Perspectives in Plant Ecology, Evolution and Systematics 16 (2014) 93–99

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Review

Diaspore dispersal ability and degree of dormancy in heteromorphic species of cold deserts of northwest China: A review

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ARTICLE INFO

Article history:
Received 16 August 2013
Received in revised form 26 January 2014
Accepted 14 February 2014
Available online 23 February 2014

Keywords:
Amphi-basicarpy
Central Asian cold deserts
Dispersal
Dormancy
Germinability
Heterocarpy
Heterodiaspory
Heterospermy

ABSTRACT

The cold deserts of northern Xinjiang Province in northwest China are rich in diaspore-heteromorphic species, and diaspore biology has been compared in more heteromorphic species native to this biogeoclimatic region than for any other region worldwide. Our primary purpose was to compare the dispersal ability and degree of dormancy in heteromorphic diaspores in Xinjiang desert plants via a review of the Chinese and English literature. We located literature on 20 heteromorphic species native to these deserts. Fourteen of the species are chenopods (Amaranthaceae). All 20 species are heterodiasporous (dimorphic, 14; trimorphic, 4; polymorphic, 2) annuals, and none is amphicarphic *sensu stricto*. Thirteen of the species are heterocarpic, six heterospermic, one amphi-basicarpic and none heteroarthrocarpic. Diaspores of 19 of the species differ in seed dormancy/germination. Thirteen of the 14 species to which both diaspore dispersal ability and degree of dormancy could be assigned had at least one morph with high (or relatively high) dispersal ability and low degree of dormancy and at least one with low dispersal ability and high (or relatively high) degree of dormancy. Conceptual models of the dynamics of seed dormancy of the two morphs for each of three dimorphic species suggest the ecological significance of heterodiaspory in the cold desert annuals. However, the ecological significance of seed/fruit heteromorphism needs to be more thoroughly demonstrated via long-term field studies that compare the life history/demography of plants derived from different morphs.

Contents

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http://dx.doi.org/10.1016/j.ppees.2014.02.004
1433-8319/

Introduction

Diaspore heteromorphism is the production by an individual plant of two or more distinct kinds of seeds and/or fruits (sometimes with accessory parts such as bracteoles, perianth or phyllary) that differ in size/mass (e.g. Dowling, 1933; Sun et al., 2008; Aguado et al., 2011); shape (e.g. Baker and O'Dowd, 1982; Venable and Levin, 1985a; Mandák and Pyšek, 1999); dispersal ability (e.g. Sorensen, 1978; Payne and Maun, 1981; Talavera et al., 2012); and/or degree of dormancy (e.g. Esashi and Leopold, 1968; Baskin and Baskin, 1976; Ruiz de Clavijo, 1994). In addition, plants produced by the different morphs differ in many ways including survival (e.g. Venable and Levin, 1985b; Imbert, 1999; Braza and Garcia, 2011); growth (e.g. Rai and Tripathi, 1982; El-Keblawy, 2003; Ruiz de Clavijo, 2001); competitive ability (e.g. Beneke et al., 1992a,b; Gardocki et al., 2000); and life history and demographic characteristics (e.g. Venable and Levin, 1985b; Venable et al., 1987).

Why should individual plants make more than one kind of seed? Plants that produce heteromorphic diaspores most commonly are annuals of disturbed sites and stressful environments such as deserts (Mandák, 1997; Imbert, 2002). Various mechanisms have evolved in annuals that are adaptations to harsh and variable environments, and seed/fruit heteromorphism is one of them. Thus, diaspores that differ in dispersal ability (e.g. with and without pappus) and germinability (i.e. nondormant vs. dormant) allow annuals to escape the harshness and unpredictability of their habitat in space (dispersal) and time (delayed germination via dormancy). The majority of studies on heteromorphism have been done on species that produce two kinds of diaspores (dimorphic). For dispersal and dormancy, it usually is found that one morph has high or relatively high dispersal ability and little or no dormancy, while the other one has low (or no) dispersal ability and high or relatively high dormancy (Venable, 1985; Ellner, 1986).

Our primary aim was to review the Chinese and English literature on dispersal ability and degree of dormancy in heteromorphic species in the cold deserts of northern Xinjiang Province, China. More specifically, for each species studied we aimed to (1) classify the heteromorphic dispersal-germination units (morphs); (2) report the number of morphs per individual, i.e. dimorphic (two morphs), trimorphic (three) or polymorphic (more than three); and (3) create a diaspore dispersal/dormancy formula based on dispersal ability and degree of dormancy.

To be included in this review, a species had to be native to the deserts of northern Xinjiang Province, China. These deserts are included in the cold deserts of Central Asia (Petrov, 1973[1976]; Walter and Box, 1983) and consist of various kinds of plant communities, such as those that occur on sand dunes and on saline-alkaline and nonsaline soils. Depending on type of soil, dominant shrubs or subshrubs and semi-arboreal genera include *Alhagi*, *Anabasis*, *Artemisia*, *Calligonum*, *Caragana*, *Ephedra*, *Halocnemum*, *Haloxylon*, *Halostachys*, *Kalidium*, *Nitraria*, *Reaumuria*, *Salsola*, *Tamarix* and *Zygophyllum*, and annual species in the Amaranthaceae (chenopods), Asteraceae, Brassicaceae, Fabaceae, Poaceae and other families may be important components of these plant communities (C.W. Wang, 1961; Hou, 1983). Several things make this review relevant to the biology of heteromorphic species. (1) Central Asian deserts are rich in taxa of Amaranthaceae (McArthur and Sanderson, 1984) previously assigned to Chenopodiaceae (APG-III, 2009). (2) With the exception of the Asteraceae, the chenopods contain more fruit/seed heteromorphic species than any other taxonomic group (Imbert, 2002). (3) A substantial amount of research has been done on heterodiasporous plants native to the deserts of northern Xinjiang, a considerable portion of which is published in Chinese.

Literature on diaspore heteromorphism of native species in Xinjiang cold deserts

Our survey identified numerous published papers and other literature on fruit/seed heteromorphism in 20 native heteromorphic species that occur in the deserts of northern Xinjiang Province in northwest China (Table 1). While most of the studies were done on plants from Xinjiang, plants of *Atriplex centralasiatica* were from Hebei Province, northern China (W. Li et al., 2008, 2011; Xu et al., 2011), *Atriplex dimorphostegia* from Israel (Koller, 1957, 1970), *Atriplex tatarica* from the Czech Republic, probably native in southeastern part of Czech Republic, i.e. southern Moravia (Mandák, 2003; Kochánková and Mandák, 2009) and *Suaeda corniculata* subsp. *mongolica* from Inner Mongolia, northern China (Cao et al., 2012; Yang et al., 2012). Further, plants of *Chenopodium album* studied were from both the United Kingdom (introduced) (Williams and Harper, 1965) and Xinjiang (native) (Yao et al., 2010a,b,c) and those of *Halogeton glomeratus* from both western USA (introduced) (Tisdale and Zappetini, 1953; Zappetini, 1953; Holl, 1954; Bruns and Rasmussen, 1958; Williams, 1960; Bruns, 1965; Cronin, 1965; Robocker et al., 1969) and Xinjiang (native) (Yu et al., 2009).

Classification of diaspore heteromorphism

With some modifications as discussed below, we follow the system of Mandák (1997) in classifying the species to kinds of diaspore heteromorphism. Mandák recognized two main categories of diaspore heteromorphic plants: heterodiaspory and amphicarpy. Heterodiasporous plants produce two or more kinds of diaspores (morphs) on aboveground shoots, and amphicarpous plants produce one or more morphs aboveground and one or more belowground. However, whereas Mandák defined heterospermy, a subcategory of heterodiaspory, as two kinds of seeds in the same fruit, we define the term as one type or more than one type of fruit (on the same individual) that contain(s) seeds that differ within or between fruits. According to Mandák, heterospermy may be combined with heterocarpy or heteroarthrocarpy, two other subcategories of heterodiaspory. Thus, to avoid this "problem" we distinguish heterocarpic and heteroarthrocarpic fruits as not having and as having distinct proximal and distal segments, respectively (see Hall et al., 2011). Further, Mandák does not use the term amphi-basicarpy, in which individual plants produce diaspores (basicarps) at ground level (not subterranean) and on higher portions of aerial stems. Thus, we follow Barker (2005) in classifying the one amphi-basicarpic species in our study and consider it to be a subcategory of heterodiaspory.

All 20 species are heterodiasporous annuals (14 Amaranthaceae, three Asteraceae, two Boraginaceae and one Brassicaceae) (Table 1), and none is amphicarpic. Further, 13 are heterocarpic, six heterospermic and one amphi-basicarpic (*Ceratocarpus arenarius*, Amaranthaceae); none is heteroarthrocarpic. Fourteen of the species produce two morphs per individual (dimorphic), four three morphs (trimorphic) and two more than three morphs (polymorphic). Plants of *Salsola brachiata* produce four dispersal-unit morphs and those of *C. arenarius* a basicarp morph without glochids (hair-like spines, generally with a barb at the tip) and a gradient of morphs with short to long glochids (without barbs) on aerial branches.

Diaspore dispersal ability

Much less research has been done on diaspore dispersal of the 20 species than on germination (see next section). Thus, relative dispersal ability of different morphs has been compared for only