Dispersal biophysics and adaptive significance of dimorphic diaspores in the annual *Aethionema arabicum* (Brassicaceae)

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**Summary**

- Heteromorphic diaspores (fruits and seeds) are an adaptive bet-hedging strategy to cope with spatiotemporally variable environments, particularly fluctuations in favourable temperatures and unpredictable precipitation regimes in arid climates.
- We conducted comparative analyses of the biophysical and ecophysiological properties of the two distinct diaspores ( mucilaginous seed (M⁺) vs indehiscent (IND) fruit) in the dimorphic annual *Aethionema arabicum* (Brassicaceae), linking fruit biomechanics, dispersal aerodynamics, pericarp-imposed dormancy, diaspore abscisic acid (ABA) concentration, and phenotypic plasticity of dimorphic diaspore production to its natural habitat and climate.
- Two very contrasting dispersal mechanisms of the *A. arabicum* dimorphic diaspores were revealed. Dehiscence of large fruits leads to the release of M⁺ seed diaspores, which adhere to substrata via seed coat mucilage, thereby preventing dispersal (antitelechory). IND fruit diaspores (containing nonmucilaginous seeds) disperse by wind or water currents, promoting dispersal (telechory) over a longer range.
- The pericarp properties confer enhanced dispersal ability and degree of dormancy on the IND fruit morph to support telechory, while the M⁺ seed morph supports antitelechory. Combined with the phenotypic plasticity to produce more IND fruit diaspores in colder temperatures, this constitutes a bet-hedging survival strategy to magnify the prevalence in response to selection pressures acting over hilly terrain.

**Introduction**

Diaspores – fruits and seeds – with specific dispersal abilities and germinabilities evolved to support the angiosperm life cycle in adaptation to the prevailing environment (Linkies *et al.*, 2010; Baskin *et al.*, 2014; Willis *et al.*, 2014). Climate change can trigger species range shifts and local extinctions, and is a global threat to plant diversity (Thuiller *et al.*, 2005; Walck *et al.*, 2011). Examples of this include the fact that global warming shifts the timing of alpine plant germination to unsuitable seasons (Mondoni *et al.*, 2012), and also that several weeds will exert additional pressure for crop–weed competition and its management (Ramesh *et al.*, 2017). For many plant species, the dispersed seed or fruit is the only phase in its life cycle when it can travel, with the potential to carry the whole plant, population, or indeed the entire species (Kesseler & Stuppy, 2012). Diaspore dispersal therefore has far-reaching demographic, ecological and evolutionary consequences (Robledo-Arnuncio *et al.*, 2014; Willis *et al.*, 2014). Knowledge of the ways in which plants disperse – and acquire the characteristics necessary for successful dispersal – has therefore been the subject of much theoretical and empirical research, dating back to observations by Linnaeus (van der Pijl, 1982) and Ridley’s (1930) seminal compilation of early dispersal studies. The diversity of morphological and biomechanical shapes and structures inherent in plant seeds and fruits is the result of the pursuit of different strategies for successful dispersal and appropriate germination timing (Baskin *et al.*, 2014; Larson-Johnson, 2016; Sperber *et al.*, 2017; Steinbrecher & Leubner-Metzger, 2017). These early life-history traits are especially important for annual plants, as they can only restart a new cycle via regeneration from the seed.

Most plant species commit themselves to monomorphism (monodispersality) as their life-history strategy, producing seeds and fruits of a single type that are optimally adapted to the respective habitat (Donohue *et al.*, 2010; Walck *et al.*, 2011; Baskin & Baskin, 2014). Interestingly, many plant species evolved a heteromorphism (heterodispersity) strategy (Imbert, 2002; Baskin & Baskin, 2014; Baskin *et al.*, 2014), a phenomenon described by...
Venable (1985) as ‘the production by single individuals of seeds (or sometimes single-seeded fruits) of different form or behaviour’. Diaspore heteromorphism is confined to 18 of 413 angiosperm families, with distinct properties having been observed not only in size, shape, and/or colour, but also in other morphological, biomechanical, and germination characteristics, the degree of dormancy, dispersal ability, mucilage production upon imbibition, and ability to form a persistent seed bank (Sorensen, 1978; Mandák & Pysek, 2001; Imbert, 2002; Lu et al., 2010; Dubois & Cheptou, 2012; Baskin & Baskin, 2014; Baskin et al., 2014). Heteromorphic diaspore traits may function as a bet-hedging strategy to cope with the spatiotemporal variability of unpredictable habitats (Slatkin, 1974; Venable, 1985).

Species with heteromorphic diaspores are most commonly annuals in dry Mediterranean and desert habitats, or in other frequently disturbed and stressful environments (Imbert, 2002). Almost all heteromorphic species of the cold deserts of northwest China are annuals (Baskin et al., 2014). Diaspores that differ in dispersal ability and germinability allow annual species to escape the harshness and unpredictability of their habitat in space and time (delayed germination via dormancy).

In the Brassicaceae family, diaspore heteromorphism has evolved independently in a few genera (Imbert, 2002; Baskin et al., 2014; Willis et al., 2014; Mohammadin et al., 2017). Distinct types of diaspore heteromorphism evolved in the genus Cakile (Cordazzo, 2006; Avino et al., 2012), in the desert annual Dipyetocarpus strictus (Lu et al., 2010, 2015), and in Aethionema arabicum (Mühlhausen et al., 2010; Lenser et al., 2016; Mohammadin et al., 2017). The genus Aethionema, the sister lineage of the core Brassicaceae, is thought to have originated and diversified in the ecologically, altitudinally, and geologically diverse Irano-Turanian region (Franzke et al., 2011; Jiménez-Moreno et al., 2015; Mohammadin et al., 2017). The dispersal of Aethionema spp. correlates with local events, such as the uplift of the Anatolian and Iranian plateaus, the formation of major mountain ranges, and probably a climatic change in seasonality towards summer aridity. Contemporary phylogenetic and biogeographic analyses identified Anatolia (Turkey) as one of the world’s hotspots of biodiversity, which includes c. 550 Brassicaceae species (Şekercioğlu et al., 2011; Jiménez-Moreno et al., 2015; Mohammadin et al., 2017). Semiarid steppe (Central Anatolian Plateau) and Mediterranean climates with dry summers (southwest Anatolia) dominate the region. The varied topography creates microclimates by elevation, including in the major mountain belts, e.g. the South Anatolian Taurus, which surround the Central Anatolian steppe. Diaspore heteromorphism evolved at least twice within the genus Aethionema, and was associated with a switch to an annual life form (Mohammadin et al., 2017).

Aethionema arabicum is a small, diploid, annual, herbaceous species whose genome sequence is published (Haudry et al., 2013). An advantage of A. arabicum as a model system for diaspore heteromorphism is that it exhibits true seed and fruit dimorphism with no intermediate morphs. Two distinct fruit types are produced on the same flowering inflorescence (infructescence): dehiscent (DEH) fruits with four to six mucilaginous (M⁺) seeds, and indehiscent (IND) fruits each containing a single nonmucilaginous (M⁻) seed (Lensert et al., 2016, 2018). Upon maturity, dehiscence of the DEH fruit morph leads to the dispersal of M⁺ seeds, while the IND fruit morph is dispersed in its entirety by abscission. Comparative analyses of the anatomy and physiology of M⁺ and M⁻ seeds, and the DEH and IND fruits that contain them, have shown a multitude of differences. These findings suggest different roles and mechanisms of the dimorphic diaspores in the dispersal and germination strategy of A. arabicum. While principal agents of diaspore dispersal include transport by wind (anemochory), water (hydrochory), animals (zoochory), and the plant itself (autochory) (Fahn & Werker, 1972), little is known about morph-specific dispersal properties and the adaptive benefits of bet-hedging mechanisms associated with heteromorphic diaspore dispersal. Thus, the structural, functional, and physiological differences in A. arabicum diaspores, underpinned by mucilage production (M⁺) and fruit coat (pericarp) restraint (IND), remain unknown.

In this study, we used a comparative approach to investigate how distinct biomechanical, hormonal, and ecophysiological properties of the diaspores (M⁺ seed vs IND fruit) influence their dispersal and ability to persist in the high-elevation scree-slope environments of Anatolia. By integrating pericarp biomechanics, flight aerodynamics, and phenotypic plasticity, we investigated the suitability of A. arabicum diaspores for dispersal by hydrochory and anemochory as two contrasting mechanisms. This is consistent with the distinct ABA content and germinability of the dimorphic diaspores. Elucidating the bet-hedging dispersal strategies in A. arabicum, and the plasticity of this dimorphism, allows us to better understand the adaptive significance of dispersal prevention and promotion mechanisms.

Materials and Methods

Seed collection and plant growth

Mature plants of Aethionema arabicum (L.) Andrz. ex DC. were grown from accession ES1020 (obtained from Eric Schranz, Wageningen University and Research Centre). Plants were grown in Levington F2 compost with added horticultural grade sand (F2 + S), under long-day conditions (16 h 20°C : 8 h 18°C, light : dark) in a glasshouse.

Diaspore biometrics and aerodynamic properties

Sixty replicates each of M⁺ seeds, M⁻ seeds extracted from IND fruits, and IND fruits were used to quantify height, width, and depth. A Leica DFC480 digital camera system, LEICA APPLICATIONS SUITE (v.4.5), and IMAGEJ (v.1.5i) were used to measure distances. The mean mass of single diaspores was determined using eight replicates of 100 individuals. Diaspore shapes were approximated as triaxial ellipsoids (M⁺ vs IND) seeds, prolate spheroids; IND fruits, oblate spheroids), in order to calculate surface area. The time taken (h) for cumulative germination to reach 50% of its maximum (T₅₀) was obtained from seed germination experiments with freshly harvested mature fruits and seeds placed in Petri dishes containing two layers of filter paper, 3 ml of dH₂O, and 0.1% (v/v) Plant Preservative Mixture (Plant Cell
Effect of diaspore on substrate attachment

Adherence potential was tested by placing diaspores on dry and water-saturated sand (grains <2 mm) in Petri dishes for 10 min. Seeds/fruits were rotated to allow whole-surface contact with the substrate, and subsequently removed. The mass of the dry seeds/fruits, including the soil particles attached to them, was compared with the mass of the same dry seeds or fruits before exposure. Three replicates each of 25 diaspores were tested.

Diaspore displacement mediated by surface water runoff

Diaspore displacement by surface water runoff was quantified using a custom-built device consisting of a container with 53 holes (400 μm diameter) above a 6°-sloped 80 × 30 cm plate, covered with 80-grit sandpaper (modified from García-Fayos et al., 2010). During each simulation, water flow was stopped after 11 had been discharged from the sprinkling head within 2.5 min. The total distance travelled by 100 replicates of each diaspore on the plate was measured.

Diaspore buoyancy

Three replicates, each of 25 diaspores, were placed on the surface of 150 ml of water contained in 250 ml Erlenmeyer flasks. Water movement in the flasks was simulated by agitation on an orbital shaker at 100 rpm (Truscott et al., 2006; Sun et al., 2012). The number of floating diaspores was counted over time.

Statistical analyses

R was used to assess the distribution of the data and test for normality and homogeneity of variance. Normal and homogeneous data were subjected to one-way ANOVA, with post hoc comparisons made by a Tukey’s honest significant difference test. The rejection threshold for all analyses was \( P < 0.05 \). Data exhibiting a non-Gaussian distribution or non-homogeneous variances were transformed by a Box–Cox (Box & Cox, 1964) transformation using the MASS package (Venables & Ripley, 2002) in R (non-transformed data are shown in all figures and tables). Analyses of diaspore behaviour on substrata were performed with a three-way ANOVA (with diaspore type, imbibition state, and sand state as main factors). Analyses of diaspore buoyancy were performed with a univariate type-III repeated-measures ANOVA (with diaspore type and time interaction included as fixed effects). All statistical analyses were conducted in R (v.3.4.2; R Foundation for Statistical Computing, Vienna, Austria) or Graphpad Prism (v.7.0a; San Diego, CA, USA).

Results

Aethionema arabicum habitat and dimorphic diaspore properties

The dimorphism of A. arabicum is characterized by the M* seed diaspores, dispersed by dehiscence, and by the IND fruit.
diaspores, dispersed by abscission (Fig. 1a). Various morphological properties that may be influencing M+ seed and IND fruit dispersal were all significantly different (Table 1). While freshly harvested mature M+ seeds germinated readily within 2 d at 14°C, IND fruit germination required at least 2–4 wk (Fig. 1b,c; Table 1). Further to this, most of the M+ seeds but none of the IND fruits germinated at 20°C, which suggests differences in dormancy and temperature responses of the dimorphic diaspores. This difference in diaspore germinability is mediated, at least in part, by a 34-fold higher ABA concentration in the IND fruits than in the M+ seeds (Table 1). This difference is associated with an ABA concentration in M+/C0 seeds that is double that in M+ seeds, combined with a very high ABA concentration of the pericarp. The low germinability of the IND fruits, therefore, seems to constitute a case of ABA-mediated and pericarp-enhanced dormancy. These differences, combined with
the observed plasticity in DEH/IND fruit ratios and numbers (Lenser et al., 2016) and the unstudied dispersal mechanisms of its dimorphic diasporas, are expected to support the adaptation of A. arabicum in its natural habitat and climate.

Aethionema arabicum is described as a poorly competitive species, and typically grows in dry locations near fields, in steppes, and on stony slopes and scree with highly eroded calcareous substrate (Fig. 1d) (Davis, 1965; Babaç, 2004; Sunar et al., 2016; Delcheva & Bancheva, 2017; Mohammadin et al., 2018). In the Anatolian peninsula, it grows at 600–2700 m elevation. Using the locations of 25 accessions, we have generated climate diagrams for the seasonal changes in precipitation, minimal and maximal temperatures at average elevation, as well as at low and high elevations (Fig.1e,f). Germination, seedling establishment, and vegetative growth occur early in spring, flowering in April to June, and fruit maturation and diapause dispersal during the dry summer and the wetter autumn (Fig.1e). The distinct morphology of the dimorphic diasporas (Table 1) suggests that they have distinct roles and biophysical dispersal mechanisms linked to the climatic regime of the region.

Dimorphic fruit biomechanics

A comparative biomechanical analysis of DEH and IND fruit valve separation at low and high RH values (simulating the dry summer and wetter autumn) revealed, first, that DEH and IND fruits differed fundamentally in their dehiscence behaviour (Fig. 2). Plant biomechanics is an integral component of the abiotic interactions of plants with gravity, wind and soil. Tensile tests determine the force needed to elongate a sample to its breaking point and provide insight into its material properties. The maximal force and the elasticity associated with separating the fruit valves were more than twofold lower for DEH than for IND fruits (Fig. 2a,b). DEH fruit force–displacement curves show a progressive failure with a sequence of force drops. This ‘composite’-type failure for DEH fruits, together with the lower maximal force, demonstrates that dehiscence is indeed the M+ seed dispersal mechanism operating for this fruit morph. Dehiscence required to disperse the M+ seeds was triggered in any humidity condition (Fig.2c). By contrast, the IND fruit diapause, for which detachment by abscission is the dispersal mechanism (Fig. 1a), shows a completely different profile. After a preloading phase, the force–displacement curve shows a linear region and no distinct plastic deformation (‘brittle’-type failure) (Fig. 2e). The maximal force and elasticity are dependent on the humidity conditions (Fig. 2c). The finding that they are significantly lower in high-humidity conditions is consistent with the role of fruit valve splitting to aid radicle emergence during IND fruit germination (Fig.1c). These contrasting biomechanical properties of the dimorphic fruits, therefore, support dehiscence and abscission, respectively, as distinct mechanisms for the M+ seed and IND fruit dispersal.

Also in agreement with IND fruit dispersal by abscission is the fact that the force required to remove dry IND fruits from A. arabicum plants is approx. six-fold lower than that required to remove dry DEH fruits (Lenser et al., 2016). To obtain evidence that this is also the case in humid conditions, to aid dispersal in autumn when precipitation increases (Fig. 1f), we investigated the effects of direct water droplet impacts on fruit abscission. While only 6 (± 1) water droplets (mean ± SE) were required to detach a ‘wet’ IND fruit by abscission, for a ‘wet’ DEH fruit, 97 (± 9) water droplets were required. In rare cases where M+ seeds were still attached to the replum after DEH fruit valve detachment had occurred (Fig. 1a), this process was also aided by rain: only 9 (± 4) water droplets were required to detach an M+ seed from the replum and, in 70% of the cases, this was achieved by a single water droplet. Dispersal by rain (ombrophorychory) is therefore a likely mechanism for the dispersal of both dimorphic diasporas, but seems more important for the abscission of the IND diapause.

IND fruits exhibit the greatest ability for wind dispersal

The wings, flat structure and large surface area (Fig. 1a,c; Table 1) of the IND fruit morph is indicative of an adaptation for dispersal by wind (anemochory). Mean descent rates (Fig. 3) of M+ seed and IND fruit diasporas, as well as for M− seeds (used as comparison to reveal the roles of the IND-pericarp), were significantly different from one another ($F_{2,297} = 438.1$, $P<0.001$). Intact IND fruits descended at the slowest rate, followed by M+ seeds (Fig. 3).

Quantified wind velocities in Anatolia are 1–4 m s$^{-1}$ (Apaydin et al., 2011), and 4 m s$^{-1}$ currents are typically used in such wind dispersal experiments. We found that, as expected, because of the
wings, IND fruits (mean \( \pm SD = 286.6 \pm 7.2 \text{ cm} \)) dispersed further than M+ seeds (78.4 \( \pm 3.7 \text{ cm} \)). In cases where M+ seeds imbibe while attached to the replum of DEH fruits (after fruit valve detachment) but do not disperse, redried M+ seeds were also included in the analysis. Dispersal of redried M+ seeds exhibited a ‘seed shadow’ with a mean distance of 197.3 cm (Fig. 4). These results demonstrate that IND fruits, with c. 3 m mean and c. 5 m maximum dispersal distance, exhibit the greatest ability for anemochorous dispersal. Although wind dispersal is more efficient over flat and uniform terrain, the IND fruit morph may have the potential for lateral and upward dispersal by gusts of wind in slope and scree habitats (Fig. 1d).

Evidence for restricted secondary dispersal (antitelechory) in M+ seeds

Once dispersed from the mother plant (primary dispersal), the behaviour and interaction of diaspores with their substrata may restrict (antitelechory) secondary dispersal, a multistep process that further extends the dispersal distance from the parent plant. Mechanisms that thereby support antitelechory may explain the contrasting differences between M+ seed and IND fruit dispersal. Assessing the behaviour of dry and imbibed A. arabicum diaspores on sandy substrate, we found striking differences between the dimorphic diaspores regarding the adherence potential of sand particles and its effects on diaspore mass. Comparisons of the initial (without contact with sand) and final (with sand particles attached) masses of the diaspores showed there was a significant interaction between the effects of diaspore morph (M+ seed vs IND fruit), state (dry vs imbibed), and sand substrate (dry vs water-saturated) on the relative increase in mass (\( F_{2.24} = 10.325, P<0.001 \)). For M+ seeds, a striking increase in mass (\( P<0.001 \)) was evident, while for IND fruits no such abundant adherence of sand particles was evident (Fig. 5). The comparison with M- seeds demonstrated that this difference is a result of the adherence

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**Fig. 2** Biomechanics of dehiscent (DEH) and indehiscent (IND) Aethionema arabicum fruits. (a, b) Comparative maximum force (\( F_{\text{max}} \)) (a) and slope (approx. modulus of elasticity) (b) required to separate fruit valves from fruits under dry conditions. (c) Comparisons of \( F_{\text{max}} \) and slope in 17%, 65% and 100% relative humidities show a trend towards gradual decrease in stiffness in both fruits, while \( F_{\text{max}} \) also decreases in the IND fruit but remains unchanged in the DEH fruit. (d, e) Characteristic force–displacement curves of mechanical tests in which fruit dehiscence occurred in A. arabicum, revealing distinct fracture biomechanical properties of slow, gradual failure of the DEH fruit (d), and sudden, complete failure for the IND fruit (e). \( n = 30 \). Error bars ± 1 SEM.

**Fig. 3** Comparative fall rates of Aethionema arabicum diaspores during descent. Mean rate of descent (m s\(^{-1}\)) of multiple mucilaginous (M+) seed diaspores and intact indehiscent (IND) fruit diaspores when released from a height of 1.08 m in still air. IND fruits required greater time to fall, confirming that the pericarp can be regarded as an adaptation for wind dispersal. The fall rates of nonmucilaginous (M-) seeds (mechanically removed from IND fruits) are shown for comparison. Differences between M+ seed and IND fruit diaspores are significant (\( P<0.001 \)). \( n = 100 \). Error bars ± 1 SEM.
As IND fruit dispersal does not appear to be restricted by surface water runoff, we wanted to compare the buoyancy potential of the A. arabicum dimorphic diaspores. There was a highly significant time × diapause type interaction ($F_{24,160} = 24.84$, $P < 0.001$; Fig. 6b) over the experimental period. The mean percentage of floating diaspores across 11 d differed significantly between M+ seeds in different states (dry, redried, imbibed) and IND fruits ($F_{3,364} = 4.3$, $P < 0.05$). Most marked differences between diaspores occurred within the first 30 min; all redried and imbibed M+ seeds were sinking rapidly, and only c. 45% of the dry M+ seeds (but 100% of the IND fruits) remained floating (Fig. 6b). Dry M+ seeds were progressively sinking (0% floating after c. 4 d), while IND fruits remained floating for many days (100% after 4 d, and > 50% after 11 d; Fig. 6b). Taken together, this comparison strongly suggests that IND fruits are adapted for dispersal in space (telechory) and time (pericarp-mediated dormancy), whereas M+ seeds possess mechanisms to remain in the direct vicinity of mother plants (antitelechory).

**Discussion**

Distinct dispersal and dormancy mechanisms of dimorphic diaspores

Our biomechanical, ecophysiological, and morphological comparison of the A. arabicum dimorphic diaspores revealed that they correspond to distinct abiotic dispersal modes and agents. The biophysical properties of the M+ seed diapause support antitelechoric mechanisms to anchor the dispersed M+ seed in the direct vicinity of the mother plant. By contrast, the biophysical properties of the winged IND fruit diapause support telechoric mechanisms (by wind and water), favouring local population dispersal over longer distances. Whereas diapause dispersal of monomorphic species can only employ the dispersal mode evolved for their single diapause type, heteromorphic species have evolved an array of distinct dispersal and dormancy adaptations, proposed to provide a bet-hedging strategy to cope with the spatiotemporal variability of their unpredictable habitats (Imbert, 2002; Baskin et al., 2013, 2014; Willis et al., 2014; Lu et al., 2015). In the Brassicaceae Cakile spp. and Dipcyphocarpus strictus, each fruit is fragmented to give rise to different morphs and, therefore, the ratio between the morphs is developmentally constrained (Cordazzo, 2006; Lu et al., 2010, 2015). By contrast, the A. arabicum dimorphic diaspores derive from distinct fruits, and both the diapause ratios and numbers can change in response to ambient temperature during reproduction (Lenser et al., 2016). The A. arabicum dimorphic system hence provides a blend of bet-hedging and plasticity, which allows it to modulate dispersal ability and germinability in response to environmental cues. We discuss here how this relates to the native habitat and climate (Fig. 1), and reveal properties of its diaspores as adaptations to distinct dispersal mechanisms.

That ABA is a key hormone, mediating the distinct environmental responses to control germination timing by dormancy mechanisms, is well established (Finch-Savage & Leubner-Metzger, 2006), but nothing was known about differences in the...
ABA content of dimorphic diaspores in *A. arabicum*. We found that a 34-fold higher endogenous ABA concentration in the IND fruit diaspore compared with the M+ seed diaspore is consistent with the low germinability (high degree of dormancy, HDo) of the IND fruit and the higher germinability (low degree of dormancy, LDo) of the M+ seed diaspore. Also, the ABA concentrations in M− seeds were higher than in M+ seeds, but much of the ABA was contained in the pericarp. High ABA concentrations controlling germination timing are also known from dry fruits of monomorphic species (Benech-Arnold *et al.*, 1999; Hermann *et al.*, 2007; Chen *et al.*, 2008). The finding of high ABA concentrations in the IND pericarp is consistent with a key role in the pericarp-mediated dormancy mechanism.

M+ seed diaspore properties support antitelechory

Flowering and reproductive development in April–June lead to diaspore dispersal during the dry summer and wetter autumn (Fig. 1e), after which the (annual) mother plant dies. In agreement with the idea that these conditions aid dispersal, our biomechanical analysis shows that M− seed dispersal via dehiscence (fruit valve separation leading to fruit opening) of DEH fruits occurs easily in both dry and humid conditions (Fig. 2). Fruit opening by dehiscence is the default trait in the Brassicaceae (Mühlhausen *et al.*, 2013), and dehiscence upon wetting has generally been associated with plants adapted to arid environments (Gutterman, 2002; Pufal *et al.*, 2010). Our finding that *A. arabicum* DEH fruit dehiscence can occur in both dry and humid conditions supports the view that M+ seed dispersal can be temporarily staggered from the late dry summer to the wetter autumn. Upon DEH fruit dehiscence, the majority of M+ seeds detach from the replum and undergo primary dispersal in close vicinity to the mother plant. Together with their lower ABA concentration and dormancy, germination of the M+ seeds will ensure the progeny sustains its presence in favourable locations.

The phenomenon of mucilage production, known as myxospermy, is commonly understood to serve as an anchorage and adherence mechanism for seed retention; it is of particular importance for species inhabiting arid regions where moisture is often a limiting factor (Yang *et al.*, 2012). We have shown that the dispersal distance of M+ seeds is significantly restricted in wet conditions (Figs 5, 6). M+ seeds have the capacity to travel only short distances via runoff water (Fig. 6a). Our findings, therefore, support the view that myxospermy provides an antitelechoric mechanism by retaining the M+ seed in favourable microclimates. Interactions with substrata provide a further means of adhesion and retention (Fig. 5). The relative increase in mass of the dry M+ seed, in particular when exposed to wet sand, illustrates the

![Graph](image_url)
effectiveness of antitelechoric seed coat mucilage production (Grubert, 1974). This repression of dispersal is an adaptive mechanism, but it does not exclude rare cases of long-distance transport by exozoochory (Mummenhoff & Franzke, 2007). Dispersal of the M+ seed diaspore therefore allows persistence in relatively stable environments by repeated establishment in few favourable sites. Nondispersed seeds may remain enclosed within DEH fruits and their spatiotemporal dispersal may be staggered by later rain events. Further analyses combining ecophysiological and genetic tools will shed light on the role and evolutionary advantages of seed coat mucilage production in A. arabicum.

Adaptive features of IND diaspores support telechory

In contrast to the M+ seed, the adaptive features of the deeper dormant IND fruit morph promote telechory by wind and water. The convergent evolution of indehisence within the Brassicaceae was associated with the evolution of pericarp features that enhance dispersal as well as an abscission zone on the joint between fruit segments in Cakile (Willis et al., 2014). Fruit traits associated with greater dispersal ability, that is, indehiscence plus pericarp features, were also associated with the evolution of larger seeds. In agreement with a greater dispersal ability (compared with the M+ seed), the A. arabicum IND fruit morph is indeed characterized by pericarp features that enhance dispersal, but it is not associated with an increased M+ seed size (Table 1). The IND fruit morph also does not contain a joint, but the abscission zone that attaches it to the plant is well developed (Lenser et al., 2016). In agreement with its dispersal by abscission (Fig. 1a), the force required to remove IND fruits from A. arabicum plants is approximately sixfold lower than that required for DEH fruits in dry conditions, and c. 16-fold lower than that for abscission triggered by rain (ombrohydrochory). This allows wind dispersal by abscission of IND fruits in dry conditions late in summer, and a further enhanced IND fruit abscission in wetter conditions in autumn. Consistent with supporting telechoric mechanisms is a wider wind dispersal kernel and a > 500-fold greater buoyancy of IND fruits compared with M+ seeds.

Although plant species with anemochorous diaspores exhibit a cosmopolitan distribution, wind dispersal in itself is regarded as a derived dispersal mechanism (van der Pijl, 1982). Structurally, the wings of the IND pericarp confer rigidity with a large surface area and low mass (Table 1). Wing-loading for IND fruits is therefore relatively low (data not shown). The

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**Fig. 6** Surface water runoff displacement and buoyancy of Aethionema arabicum fruit and seed diaspores. (a) Distance displaced by surface water runoff across a sloped sandpaper plate of dry, redried and imbibed multiple mucilaginous (M+) seeds, in comparison to indehiscent (IND) fruits. Nonmucilaginous (M-) seeds (not shown), when manually excised from the IND fruit, were displaced by 32.3 ± 1.9 cm. n = 100. Error bars ± 1 SEM. Post hoc pairwise comparisons confirmed that the dimorphic diaspores were statistically different from each other (P < 0.001). (b) Buoyancy of A. arabicum seed and fruit diaspores. Dry M+ seeds, redried M+ seeds, and imbibed M+ seeds show progressive sinking as a result of mucilage extrusion. IND fruit diaspores, by contrast, start to sink after 5 d of shaking, while all M- seeds (not shown) remained floating at the end of the experimental treatment. Symbols are offset on the x-axis for clarity. n = 3, each with 25 replicates. Error bars ± 1 SEM.
fruit valves of the pericarp comprise anatomically dead tissue filled with air which is fully permeable for water. However, the chemical constitution of the M seed coat, presence of small air pockets in the outer walls of the epidermal cells, or hydrophobic properties of the pericarp may prevent excessive moisture absorbance and confer enhanced buoyancy properties (Fig. 5b). Observations of mature infructescences during humid conditions suggest that IND fruit abscission may not be the first step in its dispersal; moisture-induced movements (hygrochasy) of fruit pedicels (Lenser et al., 2016) facilitate maximal exposure to forces enabling abscission and dispersal by wind and rain. This mechanism, present in a number of desert annuals, may correlate diasporal dispersal to rain events, which ensure optimal germination conditions (Gutterman, 1993). In addition, the presence of densely cytoplasmic cells at the base of the fruit pedicel junction in the IND fruit morph allows programmed abscission in response to such developmental and environmental cues. All these properties are consistent with IND fruit adaptations for telechoric dispersal and may be interpreted as a more opportunistic strategy to permit longer-distance range dispersal, including over the hilly terrain in the native habitat of *A. arabicum*.

**Ecological significance of *A. arabicum* diasporal dimorphism**

A complex evolutionary interdependence between dormancy and dispersal influences population structure and demography via interactions among multiple traits and selective processes (de Casas et al., 2015). The dimorphic seed dispersal strategy in *A. arabicum* represents a fascinating tradeoff between promoting telechory (IND fruit diasporas) and antitelechory (M seed diasporas). As in most described heteromorphic systems, in *A. arabicum* one of the diasporas (IND fruit) has a high degree of dormancy (HDi, i.e. low germinability), whereas the other diaspora (M seed) has a low degree of dormancy (LDo). The observed difference in germinability is consistent with our finding that the IND fruit (HDi) has a higher ABA concentration than does the M seed (LDo). Interestingly, whereas in most systems the HDi is combined with a low dispersal ability (LDi) and the LDo with a high dispersal ability (HDi) (Lu et al., 2013, 2015; Baskin et al., 2014), our biophysical and biochemical analysis of abiotic dispersal and dormancy properties revealed that this is different in *A. arabicum*. We found that the more abundant, myxospermous M seed diaspora combines LDi–LDo, while the IND fruit diaspora combines HDi–HDo. The altered dispersal and dormancy properties of the IND fruit morph are almost exclusively conferred by the distinct pericarp features and the high ABA concentration of the IND diaspora.

Dispersal and dormancy provide two bet-hedging strategies which can evolve under fluctuations in the environmental conditions in space and time (Volis & Bohrer, 2013; de Casas et al., 2015). There is extensive theoretical literature on this subject, from which the general picture emerges in many cases that these strategies are negatively associated (Buoro & Carlson, 2014; de Casas et al., 2015). One of these two strategies tends to be dominant: high dispersal associates with low dormancy, and low dispersal with high dormancy. However, much of this depends on the details of the models used. A further selective force emerges from the effects of local competition and the inclusive fitness effects that this brings. For example, in a structured deme model, in which dormancy and dispersal are allowed to evolve together, selection favours nondispersing seeds to have low dormancy (Vitalis et al., 2013). A possible explanation for the evolution of HDi/HDi morphs was hypothesized by Buoro & Carlson (2014) and de Casas et al. (2015), who argued that the joint evolution of dispersal and dormancy can be explained by environmental correlation. Spatially uncorrelated environments lead to high dispersal, and temporally uncorrelated environments to high dormancy. If indeed environments in the natural habitat of *A. arabicum* are both spatially and temporally uncorrelated, this might explain the observed pattern for the IND morph: high dormancy coupled with high dispersal.

A further, more empirically grounded, explanation is that, in *A. arabicum*, the seed ontology links HDi to HDo. The altered dispersal and dormancy properties of the IND fruit morph are almost exclusively conferred by the distinct pericarp features. In many fruit diasporas, the evolution of HDi pericarp features is associated with an increased seed size (Willis et al., 2014), but we found that this is not the case in *A. arabicum*. If selection for high dispersal variants is the dominant force, it will then go together with high dormancy. The LDi–LDo M seed and HDi–HDo IND fruit diasporas may therefore have evolved as an adaptation to semiarid habitats with varied topography, which creates microclimates by elevation in mountain belts such as the South Anatolian Taurus (Apaydin et al., 2011).

Mechanistic modelling of diasporal dispersal by wind over hilly terrain revealed that even gentle topography introduced considerable variability in the distance and direction of dispersal as a result of local turbulence (Trakhtenbrot et al., 2014). Most alpine plant species have a limited capacity for diasporal dispersal beyond 10 m, and time their germination and seedling emergence with seasonal temperature regimes (Öhwasu et al., 2007; Mondoni et al., 2012). The winged, symmetrical fruit valve membranes, together with a localized concentration of mass (M seed), contribute to high IND fruit dispersal ability in air currents. Thus, through the act of thermal convection currents and air flows typically experienced in scree slope habitats, a vertical up-current may result in a large fall time for such a winged diaspora. This contrasts with the mother-site (or safe-site) theory, originally proposed by Zohary (1937), which predicts the putative low benefit of dispersal in harsh and unpredictable environments, where dispersal and repeated establishment in local favourable sites ensure persistence of plant species and populations, but rather suggests a species that is persisting in linked sink habitats through dispersal between these sinks (Jansen & Yoshimura, 1998).

Our working hypothesis is that the plasticity of *A. arabicum* to alter the ratios and numbers of the dimorphic diasporas in response to temperature during the reproductive phase, combined with the anemochorous dispersal ability of the IND fruit diaspora, supports the longer-distance dispersal over hilly
terrain. In mountainous environments, there is considerable variation in habitat at a relatively small scale: plants at higher altitude tend to be in a more exposed, harsh and unpredictable environment that is comparatively devoid of intense competition. Ambient temperature may act as a reliable clue to a habitat’s altitude, thus allowing plants to sense which habitat they are in; by altering the ratio of seed morphs with temperature, *A. arabicum* can adjust its dispersal strategy to risks and fluctuations in the differing habitat conditions. Future ecological work in the field is required to test this hypothesis by analysing the phenology of *A. arabicum* seedling emergence and the relative numbers of the distinct dimorphic diaspores in relation to elevation.

**Conclusions**

The fascinating morphological, biophysical, hormonal and ecological adaptations of the diaspore dimorphism in *A. arabicum* reveal that they support telechory and antitelechory as contrasting dispersal strategies. The *A. arabicum* dimorphic diaspore system is distinct from most other heteromorphic species in several key features. First, it exhibits plasticity in response to the reproduction temperature in producing distinct numbers and ratios of the dimorphic diaspores. Second, for the myxospermous M*'* seed diaspore, low dispersal ability is combined with low dormancy (LDi–LDo) to support antitelechory. Third, for the IND fruit diaspore, high dispersal ability is combined with high dormancy (HDi–HDo) to support telechory by wind and water as dispersal agents. Furthermore, these key differences in the dispersal ability and germinability of the diaspores are conferred on the IND fruit diaspore by specific pericarp-derived features and high ABA concentration. Only the IND fruit diaspore can provide longer-range dispersal by wind and water. We propose that the unique features of the *A. arabicum* diaspore dimorphism and its phenotypic plasticity evolved as a bet-hedging adaptation for survival in semiarid habitats and high elevational scree-slope environments.

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**Author contributions**

KM, KS, WA, TS and GL-M planned and designed the research; KS, WA and TS performed experiments; WA, KS, TS, GL-M and KM analysed and interpreted the data; BN and VAAJ formulated the hypothesis that temperature provides the cue for elevation, leading to adaptive plasticity of diaspore ratio; WA, TS, GL-M and KM wrote the manuscript; all authors revised and approved the final article. WA, KS, GL-M and KM contributed equally to this work.

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**References**

Apaydin H, Anli AS, Ozturk F. 2011. Evaluation of topographical and geographical effects on some climatic parameters in the Central Anatolia Region of Turkey. *International Journal of Climatology* 31: 1264–1279.

Avino M, Kramer EM, Donohue K, Hammel AJ, Hall JC. 2012. Understanding the basis of a novel fruit type in Brassicaceae: conservation and deviation in expression patterns of six genes. *EvoDevo* 3: 20.

Babaç MT. 2004. Possibility of an information system on plants of South-West Asia with particular reference to the Turkish plants data service (TÜBİVES). *Turkish Journal of Botany* 28: 119–127.

Baskin CC, Baskin JM. 2014. Seeds: ecology, biogeography, and evolution of dormancy and germination. San Diego, CA, USA: Elsevier.

Baskin JM, Lu JJ, Baskin CC, Tan DY. 2013. The necessity for testing germination of fresh seeds in studies on diaspore heteromorphism as a life-history strategy. *Seed Science Research* 23: 83–88.

Baskin JM, Lu JJ, Baskin CC, Tan DY, Wang L. 2014. Diaspore dispersal ability and degree of dormancy in heteromorphic species of cold deserts of northwest China: a review. *Perspectives in Plant Ecology, Evolution and Systematics* 16: 93–99.

Benech-Arnold RL, Giallorenci MC, Frank J, Rodriguez V. 1999. Termination of hull-imposed dormancy in developing barley grains is correlated with changes in embryonic ABA levels and sensitivity. *Seed Science Research* 9: 39–47.

Box GE, Cox DR. 1964. An analysis of transformations. *Journal of the Royal Statistical Society. Series B (Methodological)* 26: 211–252.

Buoro M, Carlson SM. 2014. Life-history syndromes: integrating dispersal through space and time. *Ecology Letters* 17: 756–767.

de Casas RR, Donohue K, Venable DL, Cheptou P-O. 2015. Gene-flow through space and time: dispersal, dormancy and adaptation to changing environments. *Evolutionary Ecology* 29: 813–831.

Chen S-Y, Kuo S-R, Chien C-T. 2008. Roles of gibberellins and abscisic acid in dormancy and germination of red bayberry (*Myrica rubra*) seeds. *Tree Physiology* 28: 1431–1439.

Cordazzo CV. 2006. Seed characteristics and dispersal of dimorphic fruit segments of *Cakile maritima* Scopoli (Brassicaceae) population of southern Brazilian coastal dunes. *Brazilian Journal of Botany* 29: 259–265.
Davies PH. 1965. Flora of Turkey and the East Aegean Islands. Edinburgh, UK: Edinburgh University Press.

Delcheva MH, Bancheva ST. 2017. Aethionema arabicum Andr. ex DC. (Cruciferae) in Bulgaria – in situ and ex situ conservation. Annals of Sofia University “St. Kliment Ohridski” 101: 80–88.

Donohue K, Rubio de Casas R, Burghardt L, Kovach K, Willis CG. 2010. Germination, postgermination adaptation, and species ecological ranges. Annual Review of Ecology, Evolution, and Systematics 41: 293–319.

Dubois J, Cheptou P-O. 2012. Competition/colonization syndrome mediated by early germination in non-dispersing achenes in the heteromorphic species Crepis sancta. Annals of Botany 110: 1245–1251.

Fahn A, Werker E. 1972. Soil erosion shapes vegetation composition. In: Kozlowski TT, ed. Seed biology: importance, development, and germination. New York, NY, USA: Academic Press, 151–221.

Finch-Savage WE, Leubner-Metzger G. 2006. Seed dormancy and the control of germination. New Phytologist 171: 501–523.

Franzke A, Lyak MA, Al-Shehab IA, Koch MA, Mummenhoff K. 2011. Cabbage family affairs: the evolutionary history of Brassicaceae. Trends in Plant Science 16: 108–116.

Garcia-Fayos P, Bochet E, Cerda A. 2010. Seed removal susceptibility through soil erosion shapes vegetation composition. Plant and Soil 334: 289–297.

Grubert M. 1974. Studies on the distribution of myxospermy among seeds and fruits of Angiospermae and its ecological importance. Acta Biologica Venezuelica 8: 315–551.

Gutterman Y. 1993. Seed germination in desert plants. In: Cloudsley-Thompson JL, ed. Adaptations of desert organisms. Heidelberg, Germany: Springer, 1–253.

Gutterman Y. 2002. Seed dispersal – strategies of annual desert plants. Berlin, Germany: Springer-Verlag.

Haudry A, Platts AE, Vello E, Hoen DR, Leclercq M, Williamson RJ, Forczek Kesseler R, Stuppy W. 2012. and early Pleistocene in SW Anatolia, Turkey. Truscott AM, Soulsby C, Palmer SCF, Newell L, Hulme PE. 2006. New Phytologist 164: 1445–1451.

Haudry A, Platts AE, Vello E, Hoen DR, Leclercq M, Williamson RJ, Forczek Kesseler R, Stuppy W. 2012. and early Pleistocene in SW Anatolia, Turkey. Truscott AM, Soulsby C, Palmer SCF, Newell L, Hulme PE. 2006. New Phytologist 164: 1445–1451.

Jim Jansen VAA, Yoshimura J. 1998. Gutterman Y. 1993. Seed germination in desert plants. In: Cloudsley-Thompson JL, ed. Adaptations of desert organisms. Heidelberg, Germany: Springer, 1–253.

Jim Jansen VAA, Yoshimura J. 1998. Gutterman Y. 1993. Seed germination in desert plants. In: Cloudsley-Thompson JL, ed. Adaptations of desert organisms. Heidelberg, Germany: Springer, 1–253.

Kettermann M, Mayland-Quellhorst S, M. 2017. Mondoni A, Rossi G, Orsenigo S, Probert RJ. 2012. Climate warming could shift the timing of seed germination in alpine plants. Annals of Botany 110: 155–164.

Mühlhausen A, Lengerl T, Mummenhoff K, Theißen G. 2013. Evidence that an evolutionary transition from dehiscent to indehiscent fruits in Lepidium (Brassicaceae) was caused by a change in the control of valve margin identity genes. Plant Journal 73: 824–835.

Mühlhausen A, Bolster A, Theissen G, Mummenhoff K. 2010. Evolution of fruit dehiscence in Brassicaceae: examples from Aethionema and Lepidium. Acta Horticulturae 867: 207–219.

Mummenhoff K, Franzeke A. 2007. Gone with the bird: Late tertiary and quaternary intercontinental long-distance dispersal and allopolyploidization in plants. Systematics and Biodiversity 5: 255–260.

Ohsawa T, Tsuda Y, Saito Y, Sawada H, Lde Y. 2007. Steep slopes promote downhill dispersal of Quercus crispa seeds and weaken the fine-scale genetic structure of seedling populations. Annals of Forest Science 64: 405–412.

van der Pijl L. 1982. Principles of dispersal in higher plants. Berlin/Heidelberg, Germany: Springer-Verlag.

Pufal G, Ryan KG, Garnock-Jones P. 2010. Hydrochoric capsule dispersal in New Zealand alpine Veronica (Plantaginaceae). Annual of Sofia University “St. Kliment Ohridski” 140: 1413–1423.

Ramesh K, Matloob A, Aslam F, Florentine SK, Chauhan BS. 2017. Seeds in a changing climate: vulnerabilities, consequences, and implications for future weed management. Frontiers in Plant Science 8: Article 95.

Ridley H. 1930. The dispersal of plants throughout the world. Ashford, UK: Reeve.

Rohledo-Arnuncio JJ, Klein EK, Muller-Landau HC, Santamaria L. 2014. Space, time and complexity in plant dispersal ecology. Movement Ecology 2: 16.

Sekercioğlu ÇH, Anderson S, Akçay E, Bilgin R, Can OE, Semiz G, Tavşanoğlu Ç, Yokes MB, Soyument A, Ipekdaal K et al. 2011. Turkey’s globally important biodiversity in crisis. Biological Conservation 144: 2752–2769.

Slatkin M. 1974. Heding one’s evolutionary bets. Nature 250: 704–705.

Sorensen AE. 1978. Somatic polymorphism and seed dispersal. Nature 276: 174–176.

Sperber K, Steinbrecher T, Graeber K, Scherer G, Clausing S, Wiegand N, Hourston JE, Kurre R, Leubner-Metzger M, Mummenhoff K. 2017. Fruit fracture biomechanics and the release of Lepidium didymum pericarp-imposed mechanical dormancy by fungi. Nature Communications 8: 1868.

Steinbrecher T, Leubner-Metzger G. 2017. The biomechanics of seed germination. Journal of Experimental Botany 68: 765–783.

Sun Y, Tan DY, Baskin CC, Baskin JM. 2012. Role of mucilage in seed dispersal and germination of the annual ephemeral Alyssum minus (Brassicaceae). Australian Journal of Botany 60: 439–449.

Sunar S, Yildirim N, Sengul M, Agar G. 2016. Genetic diversity and relationships detected by ISSR and RAPD analysis among Aethionema species growing in Eastern Anatolia (Turkey). Comptes Rendus Biologies 339: 147–151.

Thullier W, Lavorel S, Araújo MB, Sykes MT, Prentice IC. 2005. Climate change threats to plant distribution in Europe. Proceedings of the National Academy of Sciences, USA 102: 8245–8250.

Trakhtenbrot A, Katul G, Nathan R. 2014. Mechanistic modeling of seed dispersal by wind over hilly terrain. Ecological Modelling 274: 29–40.

Truscott AM, Soulsby C, Palmer SCF, Newell L, Hulme PE. 2006. The dispersal characteristics of the invasive plant Mimulus guttatus and the
ecological significance of increased occurrence of high-flow events. *Journal of Ecology* 94: 1080–1091.
Venable DL. 1985. The evolutionary ecology of seed heteromorphism. *American Naturalist* 126: 577–595.
Venable WN, Ripley BD. 2002. *Modern applied statistics with S*. New York, NY, USA: Springer.
Vitalis R, Rousset F, Kobayashi Y, Olivieri I, Gandon S. 2013. The joint evolution of dispersal and dormancy in a metapopulation with local extinctions and kin competition. *Evolution* 67: 1676–1691.
Volis S, Bohrer G. 2013. Joint evolution of seed traits along an aridity gradient: seed size and dormancy are not two substitutable evolutionary traits in temporally heterogeneous environment. *New Phytologist* 197: 655–667.
Walck JL, Hidayati SN, Dixon KW, Thompson KEN, Poschlod P. 2011. Climate change and plant regeneration from seed. *Global Change Biology* 17: 2145–2161.
Willis C, Hall J, Rubio de Casas R, Wang T, Donohue K. 2014. Diversification and the evolution of dispersal ability in the tribe Brassiceae (Brassicaceae). *Annals of Botany* 114: 1675–1686.
Yang X, Baskin JM, Baskin CC, Huang Z. 2012. More than just a coating: ecological importance, taxonomic occurrence and phylogenetic relationships of seed coat mucilage. *Perspectives in Plant Ecology, Evolution and Systematics* 14: 434–442.
Zohary M. 1937. Die verbreitungökologischen Verhältnisse der Pflanzen Palästinas. *Beitraege zum Botanischen Centralblatt* 56: 1–155.

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