

Dispersal, dormancy, life history and breeding systems of southern African Asteraceae: risk-reducing strategies in unpredictable environments

By

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Declaration

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Abstract

How organisms respond to unpredictable environments is a fundamental question in evolutionary ecology. For example, plants may reduce the risk of reproductive failure by spreading their reproductive effort in space (dispersal) or in time (dormancy, iteroparity). Similarly, different plant breeding systems, (for example the ability to autonomously self-fertilise) may reduce the risk of reproductive failure in environments where pollination in particular is unreliable. Each of these strategies may be affected by selective pressures exerted by heterogeneous abiotic and biotic environments (e.g. unreliable rainfall patterns or range edge habitats). However, there is little theoretical or empirical consensus on how these strategies are related.

In Chapter 2, I explore the association between dispersal and breeding system traits and range edge proximity. I show that annual daisies from Namaqualand, South Africa, are characterised by two discreet syndromes: high selfing ability associated with good dispersal and obligate outcrossing associated with lower dispersal, regardless of range position. This chapter illustrates that selection on both breeding system and dispersal traits may act consistently across distribution ranges.

Because co-flowering plants often share pollinators, their fecundity is likely affected by changes in pollinator visitation rates or the transfer of conspecific relative to heterospecific pollen. In Chapter 3 I experimentally investigate the effects of con- and heterospecific density and spatial distribution pattern on pollination and fecundity in annual Namaqualand daisies. I show that increasing conspecific density and aggregation enhanced fecundity through increased mate availability and reduced heterospecific interference, independent of pollinator visitation rates. Moreover, I demonstrate the benefits of autonomous selfing when mates are limited and the potential for interspecific pollen transfer is high.

In Chapter 4, I examine relative investment in dispersal vs. dormancy in seed heteromorphic *Dimorphotheca* (Asteraceae) species in relation to life history, rainfall unpredictability and range edge proximity. I show annuals and perennials differ significantly in the relative investment in different dispersal strategies. However, my findings provide little support for theoretical predictions of bet-hedging strategies in unpredictable or range edge habitats. This chapter emphasises the role of local environmental factors on fruit set that may obscure expected patterns across broad climatic gradients.

Because of different costs and benefits of dispersal in space and time, we may expect negative patterns of covariation among dispersal and dormancy as alternative risk-reducing strategies. In Chapter 5, I provide evidence for a trade-off between these traits across 27 wind-

dispersed daisy species from South Africa. This trade-off did not depend on life history effects, but was inconsistent at different levels of biological organisation. I also show that the effects of life history on spatial and temporal dispersal were inconsistent.

Taken together, my research illustrates the importance of simultaneously investigating different risk-reducing strategies, because associations among them are clearly complex and often contradict theoretical expectations. Moreover I show that the effects of life history and phylogenetic relatedness cannot be disregarded. My findings underscore the importance of dispersal in space and time as well as autonomous selfing as risk-reducing responses to unreliable environments.

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*Op die groot saaidag van die heelal
het reeds 'n entjie duskant Wupperthal
oor die kaal Noordweste
'n sakkie van die Heer se beste
saad per ongeluk gelek, gelek en uitgeval*

Namakwaland ~ D.J. Opperman

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Chapter 1

Introduction

All natural environments are characterised by environmental heterogeneity. How organisms respond and adapt to unpredictable environments is a fundamental question in the study of ecology and evolution (Simons, 2011). Organisms may respond to variable environments through phenotypic plasticity (Via & Lande, 1985) or through adaptive tracking (for reviews see Childs *et al.*, 2010; Simons, 2011). Alternatively, species may rely on various risk aversion (or risk-reducing) strategies, which include evolutionary bet-hedging strategies where temporal variation in fitness is reduced at the expense of a decrease in average fitness (Slatkin, 1974; Philippi & Seger, 1989; Childs *et al.*, 2010; Ripa *et al.*, 2010). Environments are predicted to become more variable and less predictable as a consequence of global climate change (Karl & Trenberth, 2003), and species' extinction risks may be critically linked to their capacity to employ risk-reducing strategies (Childs *et al.*, 2010).

Environments can be unpredictable in space, where the habitat is divided into patches of different favourability, or in time, where the conditions of the current year or period do not resemble conditions in the previous year. Risk-reducing strategies can broadly be categorised as responses to either spatial or temporal heterogeneity. For example, dormancy, iteroparity (reproducing more than once in a life cycle) and diapause spread risk over time in response to temporal variability. These strategies are complemented by dispersal in space as fundamental evolutionary responses to environmental unpredictability (Cohen & Levin, 1991).

In my dissertation I explore the evolution of several risk-reducing strategies which may enable plant species to cope with changing environments, namely 1) dispersal, 2) dormancy, 3) seed heteromorphism, 4) longevity, and 5) autonomous selfing. Below, I briefly introduce these strategies in the context of environmental heterogeneity. I then outline expected interactions between these strategies in relation to environmental unpredictability and geographic position (see Table 1.1). I also provide background on my study system, namely wind-dispersed members of the Asteraceae family in South Africa's Succulent Karoo and Fynbos biomes. Finally, I discuss the aims of my research as well as the objectives and research questions associated with each chapter.

Dispersal

At the centre of my research is the concept of dispersal, defined as “any movement of individuals or propagules with potential consequences for gene flow across space” (Fig. 1.1a; Ronce, 2007, p. 232). Plants are sessile organisms and therefore predominantly rely on the dispersal of their propagules (e.g. seeds, fruit) to move from one location to another, for example by wind, water or animals (for reviews see Ronce, 2007; Ronce & Clobert, 2012). Consequently, dispersal is a key life history trait that may enable plants to move to more favourable environments, should the prevailing conditions be less than optimal. Dispersal ensures a more even spread of seeds in space and hence may act as risk-reducing strategy to buffer against the detrimental effects of local extinction in a particular patch (Levin *et al.*, 1984). However, in an environment with fixed spatial variation in habitat quality within the scale perceivable by the plant (i.e. its dispersal distance), dispersal cannot function as a risk-reducing strategy (Levin *et al.*, 2003; Siewert & Tielbörger, 2010). This is because dispersal tends to move individuals from occupied high quality habitats to less favourable habitats, and will therefore be selected against (Ellner & Shmida, 1981; Hastings, 1983).

In addition to spatial risk-spreading, dispersal serves numerous other functions. For example, dispersal may enable species to track their suitable habitats or to colonise new habitats, e.g. during invasions. It is of particular interest therefore to study populations on the edges of species’ distribution ranges, because individuals in these populations will make the first advances during range shifts or range expansions (Travis & Dytham, 2002; Levin *et al.*, 2003; Hughes *et al.*, 2007). However, it will also be these populations that could be most sensitive to severe climatic changes and range contractions (Sexton *et al.*, 2009). Some studies show that increased dispersal may evolve at the range edge in response to a high turnover of populations (e.g. McPeck & Holt, 1992; Darling *et al.*, 2008). On the other hand, if the cost of dispersal at the range edge is high, e.g. after recent fragmentation or on islands, reduced dispersal is predicted at range margins (Cody & Overton, 1996; Cheptou *et al.*, 2008; Dytham, 2009). In this dissertation, I address the question whether dispersal ability varies in relation to range edge proximity among populations of South African daisies, with the aim to explore these contradicting predictions.

The evolution of dispersal is driven by various selective pressures (see Table 1.1), e.g. kin competition or inbreeding avoidance (for reviews see Matthysen, 2012; Duputié & Massol, 2013). Of particular importance to my dissertation is the intuitive notion that selection for colonisation success favours dispersal ability (Richardson *et al.*, 1994; Berthouly-Salazar *et al.*, 2013).

Moreover, dispersal also has important consequences for the spatial and genetic structure of populations at local and landscape scales (Levin *et al.*, 2003). In terms of local population dynamics, shorter dispersal distances and clumped seed deposition tend to result in clumped seedling and adult distributions (Hamill & Wright, 1986; Levin *et al.*, 2003). In turn, clumped spatial distribution patterns may affect the biotic environment by altering the foraging patterns of pollinators (Hanoteaux *et al.*, 2013) or reducing the frequency of heterospecific interactions, and therefore the extent of heterospecific pollen movement (Campbell, 1986; Feinsinger *et al.*, 1986; De Waal *et al.*, 2015). The role of spatial distribution patterns in pollination success of conspecific vs. heterospecific neighbours forms one of the main questions of my research.

Dormancy

Although dispersal usually implies movement in space, it can also be viewed as movement in time, e.g. by dormant propagules (Fig. 1.1b). Dormancy (delayed germination) may buffer plants against temporal heterogeneity by ensuring that offspring survive adverse conditions in the soil seed bank, only to germinate once conditions are favourable (Cohen, 1966). This mechanism of risk-spreading may be especially important for annual plants, because their propagules are the only link to their future. If all seeds germinate at once, and conditions are detrimental for growth and reproduction (for example no follow-up rain), all of a plant's offspring could be wiped out. If germination is staggered across several seasons, the probability increases that at least some progeny will survive. As a consequence, average fitness is reduced in favour of a reduction in temporal variance in fitness so that dormancy functions as a bet-hedging strategy (e.g. Slatkin, 1974; Seger & Brockmann, 1987; Childs *et al.*, 2010; Ripa *et al.*, 2010). Indeed, dormancy in desert annuals is the canonical example of bet-hedging (e.g. Venable & Lawlor, 1980; Clauss & Venable, 2000; Venable, 2007; Gremer *et al.*, 2012). Here one may expect an increase in the proportion of dormant seeds produced as the risk associated with germination (i.e. the probability of reproductive or growth failure) increases (Table 1.1; Ellner, 1985a; Seger & Brockmann, 1987; Venable & Brown, 1988; Tielbörger *et al.*, 2012). Similarly, we may expect high dormancy to be favoured in range edge habitats, where temporal unpredictability may be high (Volis *et al.*, 2004).

In environments that are only unpredictable in space, dormancy is expected to be selected against. In this scenario, dormancy will only reduce mean fitness without reducing variance in fitness, because variance in fitness is driven by spatial and not temporal unpredictability (Venable & Lawlor, 1980; Freas & Kemp, 1983). Similarly, dormancy may be selected against in seasonal environments because rapid germination and establishment is advantageous (Yakimowski & Eckert,

2007). Alternatively, some species rely on local reproduction (seeds produced in the same patch in the previous year) as source for seedling recruitment, or the production of large seeds, xeric leaf anatomy, longevity, etc. as alternative risk-reducing strategies (Venable & Brown, 1988; Tuljapurkar, 1990; Siewert & Tielbörger, 2010) so that no relationship between dormancy and environmental unpredictability is expected (see Table 1.1). Using the proportion of dormant seeds produced by seed heteromorphic species, I ask whether relative investment in dormancy increases with increased climatic unpredictability, and at range edges.

Seed heteromorphism

Seed heteromorphism describes the production of seeds (or single-seeded fruit) of different form or behaviour (for reviews see Venable, 1985; Imbert, 2002). These propagules may differ in one or several morphological and physiological characteristics, mainly dispersal and germination requirements. Consequently, a seed heteromorphic individual can potentially spread its progeny in time and in space (Fig. 1.1c), reducing the probability of reproductive failure in heterogeneous environments. Seed heteromorphic species are therefore ideal study systems to test theoretical predictions about the evolution of dispersal and dormancy in plants.

Seed heteromorphism is present in at least 18 families of flowering plants and is particularly prevalent in the Asteraceae and Chenopodiaceae (Imbert, 2002). In the Asteraceae, differentiation between the single-seeded fruit (achenes) mainly occurs among the periphery and centre of the capitulum (Venable & Levin, 1985; Beneke, Von Teichman, *et al.*, 1992; Imbert, 1999), hereafter referred to as peripheral and central fruit. The number of peripheral florets is determined by the number of phyllotactic spirals in the capitulum, a highly canalised trait (Battjes *et al.*, 1993; Harris, 1995) and shows little plasticity. In contrast, the number of central florets is regarded as a highly plastic trait determined by the size of the capitulum and is positively correlated with the fecundity of the head (Imbert *et al.*, 1999; Imbert & Ronce, 2001). Consequently, developmental constraints may largely influence morph proportions. However, fruit and seed production in plants is also affected by local environmental effects, e.g. pollen limitation or resource availability (Campbell & Halama, 1993; Imbert & Ronce, 2001).

Life history

Selection on dispersal, dormancy and breeding systems is affected by other life history traits, in particular species' growth habit (annual vs. perennial; see predictions in Table 1.1). For example,

perennial, iteroparous plants face an increase in the probability of encountering favourable conditions for reproduction, by investing in longevity as survival strategy (Bulmer, 1985; Ehrlén & Van Groenendael, 1998; Zeineddine & Jansen, 2009). This negates the need for delayed germination to evolve in long-lived, iteroparous plants, so that dormant seed banks are predicted to be associated with annuals rather than perennials (Tuljapurkar, 1990; Rees, 1994). In addition, annuals and perennials may differ in their dispersal ability. For example, annuals may produce propagules with higher dispersal ability than their perennial counterparts (Stebbins, 1950), because their seeds are their only link to the future and spreading all offspring over a small area is risky. It has also been proposed that annuals benefit from dispersal as risk-reducing strategy because they often occur in habitats that are more unpredictable and variable (see Venable & Levin, 1983 and references therein). In addition, dispersal increases their colonising ability such as during early succession (Olivieri *et al.*, 1983; O'Connell & Eckert, 2001). In contrast, perennial species may invest more resources in longevity as survival strategy rather than dispersal ability (Ehrlén & Van Groenendael, 1998; Bossuyt & Honnay, 2006).

However, the hypothesised trade-off between dispersability and longevity (Ehrlén & Van Groenendael, 1998) is not universally accepted. For example, dispersal may be favoured in perennials because adult plants may occupy suitable patches around the mother plant so that sites for recruitment are scarce. In addition, the offspring of a perennial parent will benefit by escaping the parent's vicinity, because the chance of competition between the offspring and the larger adult plant is reduced (Cook, 1980; Venable & Levin, 1983). In a modelling study, Ronce *et al.* (2000) demonstrated that the evolutionary stable dispersal rate increases in response to kin selection when the survival rate of iteroparous adults increases. In annuals, on the other hand, there is no selection through parent-offspring competition on dispersal. Indeed, in a comparative study of several thousands of species of Asteraceae, Venable & Levin (1983) found that morphological adaptations for dispersal in space were significantly more prevalent among perennial plants than annual plants. My research investigates these aspects by comparing dispersal and dormancy ability in annual and perennial wind-dispersed Asteraceae.

Autonomous selfing

Because of their sedentary nature, most plants also rely on animal pollinators (~87.5%) or some other pollen vector (e.g. wind, ~10%) to disperse their pollen (male gametes) to stigmas (Friedman & Barrett, 2009; Ollerton *et al.*, 2011). Plant species' breeding systems (morphological and physiological aspects that govern self- vs. cross-fertilisation, e.g. self-compatibility or autogamy)

largely determines to what extent they rely on pollen vectors. In turn, biotic and abiotic ecological factors are expected to influence breeding system evolution and the degree of self-pollination expressed by plants (Darwin, 1877; Lloyd, 1979; Lloyd & Schoen, 1992; Barrett & Harder, 1996).

In animal-pollinated species, the probability of outcross-pollen receipt or reliability of pollinators will determine if populations are primarily outcrossed or self-fertilised (Lloyd, 1992; Schoen *et al.*, 1996). For example, if pollinators are absent or if pollinator abundance is low during some periods, shifts from outcrossing to autonomous self-fertilisation may be favoured because selfed seeds provide reproductive assurance (Darwin, 1877; Baker, 1955; Lloyd, 1979, 1992). The reproductive assurance hypothesis therefore predicts that autonomous selfing can evolve as risk-reducing strategy if pollinators are unreliable in delivering outcross pollen (Bond, 1994; Kalisz & Vogler, 2003; Kalisz *et al.*, 2004; Eckert *et al.*, 2006). Alternatively, autonomous selfing can assure reproduction under conditions of low mate availability (Rodger *et al.*, 2013) or when the probability of heterospecific pollen interference is high (De Waal *et al.*, 2015) – aspects that will be examined in this dissertation.

The evolution of autogamy is usually associated with a suite of morphological and functional characteristics, known as the selfing syndrome (reviewed in Sicard & Lenhard, 2011). For example, predominantly selfing species often produce smaller flowers compared to related outcrossers. In addition, they exhibit reduced pollen-to-ovule ratios and produce smaller nectar and pollen rewards. Reduced floral display could result either as a by-product of selection to increase fitness through selfing, or it may be the primary target of selection, resulting in increased selfing (Sicard & Lenhard, 2011). For example, selfing may enhance fitness when, after the transition to selfing, resources otherwise used to produce large flowers can be reallocated to for other purposes (Brunet, 1992). Alternatively, reduced flower size may result from selection for rapid maturation in ecologically marginal habitats (Guerrant, 1989) or to reduce susceptibility to florivory (McCall & Irwin, 2006). It is therefore likely that the selfing syndrome itself may function as a strategy to reduce the risk of reproductive failure associated with environmental unpredictability.

Relationships between risk-reducing strategies

Whether to move and to reproduce are two major topics in ecology and their adaptive significance is an important issue in plant population biology (Baker & Stebbins, 1965; Cheptou, 2012), because dispersal – in space (seed dispersal) and in time (dormancy and longevity) – and autonomous selfing may have major consequences for gene flow, genetic diversity, and demographic dynamics

(Duputié & Massol, 2013). Each of these strategies also involves different costs and benefits (Bonte *et al.*, 2012). Consequently, interactions and covariation among them are expected (summarised in Table 1.1 and Table 1.2), and below I highlight some of these predicted relationships in the context of environmental unpredictability and range edge proximity.

Because dispersal ability and autonomous selfing enhance colonisation success, we may expect a combination of high selfing and high dispersal ability when colonisation is favoured (the good coloniser hypothesis; De Waal *et al.*, 2014). In contrast, recent theoretical work predicts that two evolutionary stable strategies should evolve in response to spatial or temporal pollination heterogeneity in the metapopulation: an outcrossing, dispersing syndrome and a selfing, non-dispersing syndrome (the Cheptou-Massol model: Cheptou & Massol, 2009; Massol & Cheptou, 2011a). On the assumption that there is decreased availability of suitable habitat patches towards species' range edges (Holt & Keitt, 2000; Anderson *et al.*, 2009), both of these hypotheses predict interactions between geographic range position, breeding system traits and dispersal ability (Pannell & Barrett, 1998; Sun & Cheptou, 2012). However, the good coloniser hypothesis predicts selection for increased dispersal and selfing at range margins (Pannell & Barrett, 1998) whereas the Cheptou-Massol model predicts selfing ability and low dispersal at range margins (Sun & Cheptou, 2012). Very few empirical studies have tested these theoretical predictions (but see Darling *et al.*, 2008; De Waal *et al.*, 2014). My research investigates the relationship between selfing and dispersal ability, and the potential effect of range edge proximity on this relationship, in a group of annual Asteraceae.

Breeding systems are also expected to be affected by the relative importance and investment in other risk-reducing strategies. For example, inbreeding avoidance may favour an association between outcrossing and dispersal, because dispersing individuals avoid the penalties of inbreeding with closely related individuals in the same patch while gaining the benefits of outcrossing (see Auld & Rubio de Casas, 2012 and references therein). Thus, dormancy and longevity as strategies to disperse in time may be likewise associated with outcrossing (Auld & Rubio de Casas, 2012). In an influential paper, Bond (1994) argued that self-pollination, pollination by generalist fauna and escape from demographic dependence of seeds (e.g. vegetative reproduction) serve as risk-reducing strategies in environments where pollinator services are unreliable. These strategies may compensate for one another to reduce the risk of extinction. For example, if a plant is pollinated by a specialist pollinator, it faces a high risk of reproductive failure if the pollinator environment is unreliable. It may then compensate by minimising its risk of extinction, for example through the

ability to self-fertilise (e.g. De Waal *et al.*, 2012) or through a long-lived growth strategy (Boutin & Harper, 1991).

Associations between dispersal and breeding systems may also have reproductive consequences for individuals that co-flower with heterospecifics, when pollinators are shared. Because the spatial distribution patterns of individuals in a community are largely determined by the dispersal ability of propagules (Hamill & Wright, 1986; Levin *et al.*, 2003), we may expect that highly dispersive individuals may be scattered among heterospecific flowers. These individuals may suffer from a reduction in fecundity due to competition for pollinators (e.g. Rathcke, 1983), mate limitation (e.g. Kunin, 1993; Rodger *et al.*, 2013) or heterospecific pollen interference (Morales & Traveset, 2008; Ashman & Arceo-Gómez, 2013). In a recent study of annual southern African daisies, De Waal *et al.* (2014) found evidence of two syndromes: autogamy associated with high dispersal ability, and outcrossing associated with low dispersal ability. This raises the interesting possibility that the ability to autonomously self-fertilise is beneficial to dispersed individuals by assuring reproduction when mates are limited or when the probability of heterospecific interference is high.

Although dispersal serves numerous functions (for reviews see Matthysen, 2012; Duputié & Massol, 2013), the process of dispersal also carries costs, e.g. energetic costs associated with the development of morphological structures such as seed wings, risks associated with predation during the transfer stage, and risks that dispersing individuals arrive in unfavourable habitats (Bonte *et al.*, 2012; Travis *et al.*, 2012). Because selection will act to maximise fitness and minimise overall costs, trade-offs are expected among traits that influence dispersal in space or time (reviewed in Buoro & Carlson, 2014). Moreover, selection for one risk-reducing strategy may negate the need for the other (e.g. Venable & Lawlor, 1980; Klinkhamer *et al.*, 1987; but see Snyder, 2006). Indeed, negative covariation between spatial and temporal dispersal strategies, e.g. seed dispersal and dormancy, is predicted at different levels of biological organisation (reviewed in Buoro & Carlson, 2014).

The predicted interactions between longevity and dispersal or dormancy have been explained earlier in the Introduction (also see Table 1.1). For example, perennial plants face an increase in the probability of encountering favourable conditions for reproduction; and longevity is therefore an alternative temporal risk-reducing strategy to dormancy (Bulmer, 1985; Ehrlén & Van Groenendael, 1998; Zeineddine & Jansen, 2009). Of particular interest is the effect of longevity on covariation between dispersal and dormancy. For example, we may expect that patterns of

covariation between dispersal and dormancy may vary when comparing annual vs. perennial species, because of different selective pressures on dispersal and dormancy imposed by different life histories. Here, I address the question whether a trade-off between dispersal and dormancy is evident at the individual-, population- and species-level across annual and perennial Asteraceae.

Study system

My research is centred in the winter-rainfall region of southern Africa, which includes the mesic Cape Floristic Region and the arid Succulent Karoo biome (the Greater Cape Floristic Region; Born *et al.*, 2007). Both of these regions are biodiversity hotspots (Myers *et al.*, 2000). The Greater Cape Floristic Region (GCFR) is dominated by two vegetation types: Fynbos in the mountains on oligotrophic soils derived from sandstones and granites, and Succulent Karoo on the plains and on more eutrophic soils derived from shale or rarely granites (Born *et al.*, 2007 and references therein). In the CGFR, winter rainfall (April – September) is regarded as the most ecologically significant variable for germination and flowering (Cowling *et al.*, 1999).

The majority of my work was conducted in Namaqualand, an ethnogeographical region within the Succulent Karoo biome. Namaqualand is a climatically moderate desert and has a unique climate characterised by two rainfall gradients (Desmet & Cowling, 1999): a gradual decrease in annual precipitation toward the north into the southern Namib Desert, and a longitudinal gradient in seasonality with winter rainfall along the west coast and summer rainfall in the interior (Desmet, 2007). Although rainfall in the region is low [(50) 100-250 (400) mm pa] and occurs mainly during winter, it is considered relatively reliable when compared to other regions with similar mean annual precipitation (Cowling *et al.*, 1999; Desmet, 2007). Nevertheless, a gradient of decreasing winter rainfall predictability is evident from south to north and from west to east (Desmet & Cowling, 1999; C. de Waal, unpubl. results).

Although Namaqualand is characterised by a remarkable diversity of dwarf succulents and geophytes, the region is most famous for its spectacular displays of spring annuals, a popular tourist feature (Fig. 1.2; Van Rooyen, 1999). Following the winter rains, multiple species germinate and flower in the relatively short growing season, often forming dense co-flowering communities, particularly in disturbed sites (Cowling, Esler & Rundel 1999). These communities consist predominantly of various native Asteraceae species and are often dominated by a single species (usually *Ursinia* or *Dimorphotheca* species) with other species scattered in between at lower densities (C. de Waal, pers. obs).

Many plant species in Namaqualand's spring-flowering communities are characterised by open flowers and inflorescences (e.g. Asteraceae and Mesembryanthemaceae), which make their rewards accessible to a wide range of insects. The pollinator community in the region is dominated by a diverse assortment of insects with generalist visitation tendencies; predominated by bees, bee-flies and monkey-beetles (Struck, 1994; Ellis & Johnson, 2009; De Jager & Ellis, 2014).

Megapalpus capensis (Bombyliidae), a key pollinator of orange daisies, does not exhibit floral constancy (Ellis & Johnson, 2012). Despite the rich supply of floral reward during the flowering season, some authors have suggested that the abundance of flower-visiting insects is relatively low (Struck 1994; Esler 1999).

The Asteraceae of the Greater Cape Floristic Region are ideal model systems to address my research questions (see below). The Asteraceae comprises the largest family of flowering plants in the region, allowing comparisons between sufficient numbers of closely related species representing different life histories. The majority of these species produce fruit which are adapted for wind dispersal, allowing direct comparisons of dispersal ability within the same dispersal syndrome. Moreover, these species exhibit geographic variation in traits associated with risk-reducing strategies, such as dispersal traits, dormancy and seed heteromorphism. Their distribution ranges cover environmental gradients that are of relevance to this study, specifically gradients of rainfall unpredictability.

Very little is known about risk-reducing strategies in Namaqualand. This is surprising, given that plant diversity in the region might be particularly vulnerable to anthropogenic climate change (Midgley & Thuiller, 2007). In a series of studies (e.g. Beneke, Van Rooyen, *et al.*, 1992; Beneke, Von Teichman, *et al.*, 1992; Beneke *et al.*, 1993), seed heteromorphism was investigated in members of the genus *Dimorphotheca* (Asteraceae). In *Dimorphotheca*, winged achenes (adapted for wind dispersal) originate from the disk florets and typically germinate quickly and easily, resulting in robust and highly competitive individuals. On the other hand, peripheral achenes, originating from the ray florets, do not possess dispersal structures and dormancy seems to be induced by the physical and chemical qualities of the relatively thick pericarp. Consequently, dispersal in space and time by the offspring of the same individual may reduce the risk associated with spatial and temporal heterogeneity. However, these studies focused only on plants from a single locality and only investigated morph characteristics of two annual species (*D. sinuata* and *D. polyptera*).

Research objectives

The main objective of this dissertation is to investigate variation in strategies – particularly dispersal, dormancy, seed heteromorphism, longevity and autonomous selfing – that may reduce the risk of reproductive failure in unpredictable environments (for example in conditions of rainfall unpredictability or close to species' range edges), or where pollination is unreliable. Moreover, I aim to explore ecologically important relationships among these strategies. Specifically, I investigate the hypothesis that selection pressures exerted by climatic unpredictability or range edge habitats affect the relative investment in dispersal in space vs. dispersal in time. Although theoretical predictions for interactions and covariation among various risk-reducing strategies abound (for reviews see Auld & Rubio de Casas, 2012; Cheptou, 2012; Buoro & Carlson, 2014), empirical evidence is relatively rare and often conflicting (see Tables 1.1 and 2.1). My dissertation directly aims to contribute much needed empirical tests of these theoretical predictions by measuring wind dispersal ability and dormancy (and investment in dispersive vs. dormant propagules in seed heteromorphic species) and breeding systems across the geographic distribution ranges of numerous native annual and perennial African daisies from the GCFR (Chapters 2, 4 and 5). Moreover, using a novel set of experiments, I aim to tease apart the density- and dispersion-dependent mechanisms that affect fecundity of daisies co-flowering with heterospecifics in spring flowering communities (Chapter 3). Below I state the objectives and research questions of each data chapter.

Chapter objectives and research questions

Chapter 2: Dispersal and breeding system traits are both thought to play a significant role in the ability of plants to colonise new habitats and maintain founder populations. Because species have attained their present distribution ranges through colonisation, we may expect these traits to vary geographically. Several theories predict associations between dispersal ability, selfing ability and the relative position of a population within its geographic range (e.g. Pannell & Barrett, 1998; for reviews see Auld & Rubio de Casas, 2012; Sun & Cheptou, 2012). However, there is little theoretical or empirical consensus on exactly how these variables are related (Table 2.1). The objective of Chapter 2 was to provide an empirical investigation of these contradicting, but testable, predictions (outlined in Table 2.1) by investigating dispersal ability and selfing ability in central vs. range-edge populations of 13 annual, wind-dispersed Asteraceae species from Namaqualand. Specifically, I ask 1) to what extent are these species capable of self-fertilisation? 2) Do range-edge

and central populations differ in dispersal ability and selfing ability? 3) Is there a relationship between selfing ability and dispersal ability?

Chapter 3: The effects of pollinator-mediated interactions on plant fecundity are usually attributed to changes in pollinator visitation rates. However, mechanisms that involve the transfer of conspecific relative to heterospecific pollen, independent of visitation rates, receive relatively less attention. The relative importance of various pollinator-mediated interactions may depend on the density, relative abundance and spatial arrangement of con- and heterospecifics (Feinsinger *et al.*, 1991; Stoll & Prati, 2001; Hanoteaux *et al.*, 2013) and is rarely considered in the context of component Allee effects.

In Chapter 3 I explored the effects on con- and heterospecific density and dispersion on pollination visitation rates and fruit set within and between two annual, co-flowering self-incompatible daisies (*Dimorphotheca pinnata* and *U. cakilefolia*), as well as comparisons with an autogamous selfer *U. anthemoides*. These species co-occur in the dense communities that form Namaqualand's famous spring flowering displays (Fig. 1.2). I link this work with the findings of Chapter 2 by taking into account the role of dispersal in generating clumped vs. dispersed spatial distribution patterns, which will affect the relative importance of various pollinator-mediated mechanisms (Table 3.3), as well as the association between dispersal ability and autogamy among southern African daisies (De Waal *et al.*, 2014). Specifically, I ask 1) what are the effects of absolute density, relative abundance, and dispersion pattern on pollinator visitation rates to each co-flowering species?; 2) What are the effects of these factors on plant fecundity (fruit set)?; 3) Do changes in pollinator visitation rates, if present, explain variation in fruit set in relation to density and dispersion patterns?; 4) Does self-compatibility offer reproductive assurance to scattered individuals at low density?

Chapter 4: The aim of Chapter 4 is to explore relative investment in dispersal vs. dormancy as risk-reducing strategies in the seed heteromorphic genus *Dimorphotheca*. Specifically, I investigate the relative production of central, dispersive (mainly non-dormant) propagules vs. peripheral, non-dispersive (mainly dormant) propagules in three annual vs. two perennial species. In two annuals, I also test for predicted associations between investment in dispersal and dormancy with rainfall unpredictability and range edge proximity (Table 1.1), taking into account the effects of inflorescence size (i.e. the number of florets) on fruit set. I addressed the following questions: 1) Do annual and perennial species differ in their production of dispersive, non-dormant (central) vs. non-dispersive, mainly dormant (peripheral) fruit? 2) Is there significant geographic variation among

populations of the annual *D. sinuata* and *D. pluvialis* in the production of ray vs. disk florets and peripheral vs. central fruit? 3) Can winter rainfall unpredictability predict variation in floret and/or fruit ratios of *D. sinuata* and *D. pluvialis*? 4) Do populations on the range edge vs. range centre differ in their relative investment in dispersal and dormancy?

Chapter 5: My final data chapter follows a recently published review (Buoro & Carlson, 2014) which provided clear theoretical hypotheses for covariation in dispersal in space and time. In general, negative covariation between spatial dispersal and dormancy are expected at different levels of biological organisation. Although the Buoro and Carlson (2014) review includes relevant empirical studies, the authors point out that empirical tests of theoretical predictions are very limited and often conflicting. Moreover, they highlight gaps in the literature, e.g. studies that simultaneously investigate covariation in dispersal and dormancy in nature at different levels of biological organisation and studies that incorporate other risk-spreading strategies such as longevity (which also spreads risk in time).

My final chapter directly aims to address these knowledge gaps by exploring relationships between seed dispersal (wind dispersal ability) and dormancy in annual and perennial species across six genera of southern African Asteraceae at the individual-, population- and species-level. I asked: 1) Are there consistent differences in seed dispersal and dormancy among annual and perennial species? 2) Is the probability of germination larger for more dispersive fruit (i.e. individual-level)? 3) Is there evidence for negative covariation (i.e. a trade-off) between seed dispersal and dormancy across populations within species? 4) Is there evidence for trade-offs between seed dispersal and dormancy across species? I also explored whether patterns of covariation varied among annual and perennial species.

Table 1.1. Prevalent and often conflicting hypotheses predict different associations between environmental unpredictability and growth habit with investment in dormancy and allocation to dispersal, as well as varying effects of range position on these traits. Examples of theoretical and empirical references that are consistent with each set of predictions are provided. Note that this is not intended to be a complete review of the literature related to this subject.

| Prediction | Reason for prediction | Examples of theoretical predictions | Examples of empirical support |
|--|---|---|---|
| <i>Association between dormancy and environmental unpredictability</i> | | | |
| Positively correlated | If environment is unpredictable in time, dormancy acts as bet-hedging strategy by spreading risk across years | Cohen, 1966; Venable & Lawlor, 1980; and references therein Seger & Brockmann, 1987 | Clauss & Venable, 2000; Venable, 2007; Gremer <i>et al.</i> , 2012; Tielbörger <i>et al.</i> , 2012 |
| Negatively correlated | If environment is only unpredictable in space, dormancy will only reduce mean fitness without reducing variance in fitness | Venable & Lawlor, 1980 | Freas & Kemp, 1983 |
| No association | Rely on local reproduction as source for seedling recruitment; production of large seeds, xeric leaf anatomy, etc. as buffering mechanisms | Venable & Brown, 1988 | Siewert & Tielbörger, 2010 |
| | Environmental cues that break dormancy are uncorrelated with conditions that permit successful maturation | Venable & Lawlor, 1980 | † |
| <i>Association between dispersal and environmental unpredictability</i> | | | |
| Positively correlated | Dispersal spreads risk if environment is spatially unpredictable and rare | Levin <i>et al.</i> , 1984; Snyder, 2006 | E.g. pioneer species in primary successions, see references in Bakker <i>et al.</i> , 1996 |
| Negatively correlated | Temporal and/or spatiotemporal heterogeneity – dispersal less efficient to spread risk; selection for risk-reducing strategies decrease with increase in environmental predictability | Hastings, 1983; Cohen & Levin, 1991; Snyder, 2006 | Ellner & Shmida, 1981; see references in Bakker <i>et al.</i> , 1996 |
| No association | Dispersal not important risk-reducing mechanism in unpredictable environments | † | Siewert & Tielbörger, 2010 |

Association between dormancy and dispersal in relation to environmental unpredictability

| | | | |
|-----------------------|--|--|---|
| Positively correlated | In environments that are rare both in time and space (negative autocorrelation), dormancy reduces risk of reproductive failure for seeds that are dispersed to temporally unfavourable sites (reduces cost of dispersal) | Cohen & Levin, 1991; Snyder, 2006 | See Bakker <i>et al.</i> , 1996 and references therein |
| Negatively correlated | Costs associated with both dispersal and dormancy, so a trade-off is predicted | Venable & Lawlor, 1980; Klinkhamer <i>et al.</i> , 1987; Venable & Brown, 1988 | Rees, 1993; Ehrlén & Van Groenendael, 1998; see references in Buoro & Carlson, 2014 |
| No association | Other traits facilitate successful survival to reproduction in unpredictably varying environments | E.g. seed size, Venable & Brown, 1988 | E.g. xeric leaf morphology, Siewert & Tielbörger, 2010 |

Effect of growth habit on dispersal ability

| | | | |
|------------------------------|---|---|---|
| High dispersal in perennials | Dispersal favourable because sites for recruitment are scant, to avoid kin competition | † | Cook, 1980; Soons & Ozinga, 2005 |
| Low dispersal in perennials | Trade-off between colonisation ability and the ability to escape extinction; longevity reduces variance in reproductive output, lowers advantage of dispersal | See references in Ehrlén & Van Groenendael, 1998; Palmer & Strathmann, 1981; Bossuyt & Honnay, 2006 | Ehrlén & Van Groenendael, 1998; Andersen, 1992 |
| High dispersal in annuals | Enhance colonisation success | Levin <i>et al.</i> , 1984 | Olivieri <i>et al.</i> , 1983; O'Connell & Eckert, 2001 |
| | Annuals inhabit more uncertain and variable habitats where dispersal is favoured | Stebbins, 1950; Baker, 1974 | Stebbins, 1950; Ehrendorfer, 1965; Baker, 1974 |
| Low dispersal in annuals | Prevent movement of descendants out of favourable patch | Levin <i>et al.</i> , 1984 | See Ellner & Shmida, 1981 and references therein |

Effect of growth habit on capacity for dormancy

| | | | |
|-----------------------------|--|------------------------|----------------------|
| High dormancy in perennials | High variation in fecundity of long-lived adults | Rees, 1993 | Parker & Kelly, 1989 |
| Low dormancy in perennials | Invest in longevity to spread risk in time; little variation in fecundity of | Rees, 1993; Rees, 1994 | Rees, 1993 |

long-lived adults

Larger seeds in perennials lead to high rates of loss to herbivores, which selects against dormancy; alternatively, larger seeds have more resources to establish in unfavourable conditions, reducing realised variance in habitat quality which selects against dormancy

Venable & Brown, 1988

Thompson, 1987; Rees, 1993

| | | | |
|--------------------------|--|-------------------------------------|---|
| High dormancy in annuals | Reduce temporal variance in individual fitness; spread risk in time | Cohen, 1966; Bulmer, 1984 | Clauss & Venable, 2000; Venable, 2007; Freas & Kemp, 1983 |
| Low dormancy in annuals | Does not reduce variance in fitness if environment is highly predictable | Venable & Lawlor, 1980 | Freas & Kemp, 1983 |
| | Trade-off with dispersal as risk-reducing strategy | Cohen, 1967; Venable & Lawlor, 1980 | Ehrlén & Van Groenendael, 1998 |

Effect of range position on dispersal (from De Waal et al. 2014)

| | | | |
|---------------------------|---|--|--|
| High dispersal at margins | Expanding range margin, for example during invasion | Travis & Dytham, 2002; Hughes et al., 2007 | Phillips et al., 2006; Hughes et al., 2007 |
| | High turnover of populations | McPeck & Holt, 1992; Dytham, 2009 | Darling et al., 2008 |
| Low dispersal at margins | High cost of dispersal (e.g. islands, recent fragmentation) | McPeck & Holt, 1992; Dytham, 2009 | Cody & Overton, 1996; Cheptou et al., 2008 |

Effect of range position on dormancy

| | | | |
|--------------------------|--|---|---|
| High dormancy at margins | Temporally unpredictable environments at range margin | † | Volis et al., 2004 |
| Low dormancy at margins | Rapid germination (and establishment) may be adaptive in seasonal environments | † | Kluth & Bruelheide, 2005; Yakimowski & Eckert, 2007 |

†Lack of either empirical or theoretical studies to support the particular prediction.

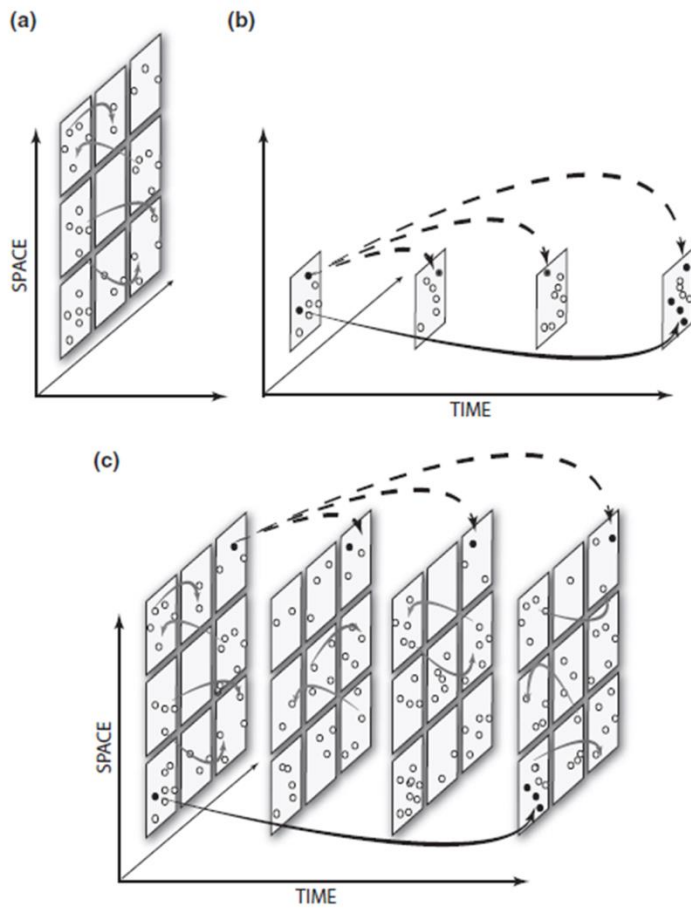


Fig. 1.1. Dispersal in space and time. These panels illustrate (a) spatial dispersal within a generation (solid grey arrows); (b) Temporal dispersal (between generations), which can be achieved through e.g. iteroparity (dashed black arrows) or dormancy (solid black arrow); and (c) combinations of dispersal through space and time. From Buoro & Carlson 2014, *Ecology Letters*. © 2014 John Wiley & Sons Ltd/CNRS



Fig. 1.2. Examples of the striking floral displays of spring annuals in Namaqualand, South Africa.

Chapter 2

Selfing ability and dispersal are positively related, but not affected by range position: a multi-species study on southern African Asteraceae

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Abstract

Dispersal and breeding system traits are thought to affect colonisation success. As species have attained their present distribution ranges through colonisation, these traits may vary geographically. While several theories predict associations between dispersal ability, selfing ability and the relative position of a population within its geographic range, there is little theoretical or empirical consensus on exactly how these three variables are related. We investigated relationships between dispersal ability, selfing ability and range position across 28 populations of 13 annual, wind-dispersed Asteraceae species from the Namaqualand region of South Africa. Controlling for phylogeny, relative dispersal ability – assessed from vertical fall time of fruits – was positively related to an index of autofertility – determined from hand-pollination experiments. These findings support the existence of two discrete syndromes: high selfing ability associated with good dispersal and obligate outcrossing associated with lower dispersal ability. This is consistent with the hypothesis that selection for colonisation success drives the evolution of an association between these traits. However, no general effect of range position on dispersal or breeding system traits was evident. This suggests selection on both breeding system and dispersal traits acts consistently across distribution ranges.

Introduction

Dispersal and breeding system characteristics vary across the geographic ranges of species and may play a significant role in the ability of plants to colonise and maintain founder populations. Evolutionary associations between dispersal ability and breeding system are expected, because both traits directly affect gene flow, colonisation dynamics and possibly adaptive potential within metapopulations. Studies investigating these associations have led to numerous, and often conflicting, predictions (Table 2.1; for reviews see Auld & Rubio de Casas, 2012; Cheptou, 2012). Similarly, our understanding of geographic variation of dispersal ability and breeding system traits also appears to be underpinned by contradictory hypotheses (Table 2.1).

In a seminal paper, Baker (1955) argued that, because of mate or pollinator limitation following long distance dispersal, the ability to self-fertilise should improve colonisation success by assuring reproduction (“Baker’s Law”: Stebbins 1957; Baker 1967; Darwin 1876; Lloyd 1979, 1992). Because dispersal ability also increases the probability of successful colonisation, it is intuitive to expect a combination of high selfing and high dispersal ability when colonisation is favoured (referred to as “the good coloniser syndrome” by Cheptou & Massol, 2009) and lower selfing ability and lower dispersal ability when it is not. We shall refer to this extension of Baker’s Law as the good coloniser hypothesis.

Diverse studies have provided support for the importance of selfing ability during colonisation. Reproductive assurance through self-fertilisation has often been documented (e.g. Kalisz *et al.*, 2004; reviewed in Eckert *et al.*, 2006). Furthermore, the prevalence of self-compatibility is unusually high among island taxa (Baker, 1955, 1967; McMullen, 1987; Anderson *et al.*, 2001; Bernardello *et al.*, 2001; but see Carr *et al.*, 1986) and invasive plants (e.g. Rambuda & Johnson, 2004; van Kleunen *et al.*, 2008). Self-fertilisation also alleviates the effects of inadequate pollinator and mate availability on fecundity during invasion (Davis *et al.*, 2004; Van Kleunen *et al.*, 2007; Rodger *et al.*, 2013). Even in native plants, recently established populations may be more outcross pollen limited than well-established populations (Brys *et al.*, 2013). Similarly, dispersal ability has been shown to enhance invasion success (Richardson *et al.*, 1994; Berthouly-Salazar *et al.*, 2013). Models of metapopulation dynamics also suggest that the good coloniser syndrome should be selected for under metapopulation conditions, where frequent local extinction is countered by recolonisation (Pannell & Barrett, 1998).

In contrast to the good coloniser hypothesis, recent theoretical work predicts that two evolutionary stable strategies should evolve in response to spatial or temporal pollination heterogeneity in the metapopulation: an outcrossing, dispersing syndrome and a selfing, non-dispersing syndrome (the Cheptou-Massol model: Cheptou & Massol, 2009; Massol & Cheptou, 2011a). Within the framework of this model, pollination uncertainty poses a severe threat to outcrossing plants incapable of dispersing to more favourable patches. This can be alleviated by evolving self-fertilisation, the cost of which is inbreeding depression, or by evolving dispersal, the cost of which is loss of progeny that do not reach favourable sites. In these models, paying the costs of both dispersal and inbreeding is greater than either cost alone (i.e. self-fertilisation and non-dispersal, or outcrossing and high dispersal), preventing selection for dispersive selfers (Massol & Cheptou, 2011b).

As the joint evolution of selfing and dispersal ability has seldom been considered, there are few data sets exploring the relationships between them. However, consistent with the Cheptou-Massol model, species that are likely to be more attractive to pollinators and therefore more likely to be outcrossed, also tend to produce larger fruits that are more attractive to dispersers (Primack, 1987). Similarly, dioecious species, which are obligate outcrossers, often produce fleshy fruits effective for long-distance dispersal (Bawa, 1980; Givnish, 1980).

On the assumption that there is decreased availability of suitable habitat towards range margins (Holt & Keitt, 2000; Anderson *et al.*, 2009), both the good coloniser hypothesis and the Cheptou-Massol model predict associations between geographic range position, breeding system traits and dispersal ability (Pannell & Barrett, 1998; Sun & Cheptou, 2012). However, they predict opposite associations. Under the good coloniser hypothesis, reduced availability of suitable habitat towards range margins should lead to increased selection for colonisation, resulting in selection for increased dispersal and selfing ability at range margins (Pannell & Barrett, 1998). Another possibility is that decreased abundance of specialist pollinators towards range margins could result in increasing pollen limitation and selection for selfing along range margins (Sun & Cheptou, 2012). This has been confirmed in a number of species (e.g. Barrett *et al.*, 1989; Moeller & Geber, 2005; Eckert *et al.*, 2006; Michalski & Durka, 2007; but see Herlihy & Eckert, 2005). Increased dispersal may also evolve in peripheral populations when species' range margins are expanding (Travis & Dytham, 2002; Phillips *et al.*, 2006; Hughes *et al.*, 2007) or when local extinction is common (McPeck & Holt, 1992; Dytham, 2009). In contrast, reduced dispersal at range margins may evolve when the cost of dispersal is high, as is the case on small islands (Cody & Overton, 1996) or after recent fragmentation (Cheptou *et al.*, 2008).

An extension of the Cheptou-Massol model (Sun & Cheptou, 2012), examined the geographical distribution of the selfing/dispersing association in response to environmental gradients. They demonstrated that gradients of increased pollen limitation, decreased habitat availability and decreased inbreeding depression from range centres to range margins could lead to an association between outcrossing and high dispersal in range centres and an association between selfing and low dispersal at range margins (Sun & Cheptou, 2012). We are only aware of one study which has tested these predictions by measuring selfing ability and dispersal ability in range-edge and central populations, and this was only done for a single species. This detailed investigation of the dune plant *Abronia umbellata* supported the good coloniser hypothesis rather than the Cheptou-Massol model (Darling *et al.*, 2008).

Here we investigate dispersal ability and breeding system parameters of range-edge and central populations in multiple annual Asteraceae species in Namaqualand, South Africa. We ask: 1) to what extent are these species capable of self-fertilisation? 2) Do populations from the range margins and the central parts of the range (range-edge and central populations) differ in dispersal ability and selfing ability? 3) Is there a relationship between selfing ability and dispersal ability? Such empirical investigations of the testable predictions summarised in Table 2.1 are essential to resolve the debate on (co)variation in breeding system and dispersal traits.

Materials and methods

Study species and sampling

Thirteen annual Asteraceae species were sampled in their native distribution ranges in the arid Namaqualand region of the winter-rainfall Succulent Karoo biome, South Africa. These species flower during late winter and spring (July – September) and produce achenes adapted for wind dispersal. Sampling took place in August – September 2012.

Where possible, we included at least one central and one range-edge population of each species (Table S2.1). Range margins were established from our own extensive sampling as well as herbarium record entries listed in the South African National Biodiversity Institute's Integrated Biodiversity Information System (sibis.sanbi.org). Range-edge populations were identified as the last population encountered for at least ten kilometres when traversing the probable range margin of a species as indicated on its distribution map. The coastal margin was not used for species that

extended to the Atlantic Ocean. Dispersal and breeding system traits were measured for each population, except for *Ursinia calenduliflora* (Table S2.2). For this species, we did not have fruit available for dispersal measurements from the population used for the breeding system study (data provided by M.L. de Jager). Instead, we used means of dispersal ability from four different populations, also in the range centre.

Controlled pollination experiments

For all species except *Ursinia calenduliflora*, plants were collected from the field, transferred to containers filled with soil from the same site and maintained at the Succulent Karoo Knowledge Centre in Kamieskroon, Northern Cape, in a pollinator exclusion tent made from nylon mesh. Three pollination treatments were applied to each species: hand cross-pollination, hand self-pollination, and unmanipulated (= autonomous self-pollination). Only one treatment was applied per plant to a single inflorescence. For the hand cross- and hand self-treatments, all receptive stigmas on the inflorescence were pollinated once with pollen from another or the same individual, respectively, except for *Dimorphotheca sinuata* and *D. pluvialis* where each inflorescence was pollinated on two occasions. For *U. calenduliflora* the same pollination treatments were applied as described above, but these were carried out in a greenhouse at the University of Stellenbosch (De Jager & Ellis, 2014). Mature infructescences were collected and the number of fruit scored. For some populations, infructescences were not fully mature when the experiment was terminated. We therefore scored all swollen ovaries as fruit. Although this means that some late-aborted embryos could have been scored as fruit, scoring was consistent across species and populations harvested at different stages of fruit development.

To assess the ability to self-fertilise, breeding system indices were calculated from fruit set data for each population as follows: 1) an index of autofertility (AF_X) was calculated as autonomous self-pollination/hand cross-pollination (the subscript 'X' represents the cross pollination term in the denominator, as autofertility is sometimes calculated with natural or self-pollination in the denominator), and 2) an index of self-incompatibility (ISI) was calculated as $1 - \text{hand self-pollination/hand cross-pollination}$. AF_X represents the proportion of maximum fruit set that can be achieved by autonomous self-pollination, and is a measure of independence of plants from pollinators and mates. ISI and AF_X values sometimes exceeded the theoretical range of 0 - 1. Changing these values to 0 or 1 did not affect results, and we present analyses based on the original values.

AF_X and ISI were highly (negatively) correlated ($r^2 = 0.93$), and analyses yielded similar results. Here we present results for AF_X , where positive AF_X values reflect the ability of plants to self-pollinate and have the resulting self-pollen fertilise ovules. ISI results are reported in Figs. S2.5-S2.6. A potential explanation for the tight correlation between ISI and AF_X is that in the disk florets of daisies, pollen is presented on the reverse side of the stigma. The proximity of pollen to the receptive area of the stigmas in hermaphrodite florets ensures that autonomous self-pollination readily takes place, with self-fertilisation and fruit set ensuing if plants are self-compatible.

Dispersal measurements

We collected a bulk sample of mature fruits from at least five randomly chosen individuals per population for all species, except *Dimorphotheca*. Twelve to 30 fruits (mean = 29) were randomly selected from each bulk sample and used for subsequent dispersal measurements. For *Dimorphotheca* species, which are seed heteromorphic, we collected mature seed families from ten randomly chosen individuals per population. We selected 50 achenes per morph per population in the dimorphic *D. sinuata* and *D. pluvialis*, and 30 achenes per morph per population in the trimorphic *D. polyptera*.

To determine the relative wind-dispersal capacity of each population, we used a digital stopwatch to measure the time it took each fruit to fall to the ground when released at the top of a transparent Perspex tube (fall time). The tube measured 2.54 m in length and 0.21 m in diameter and was closed at the top except for a small hole in the centre through which fruits were released. The same observer recorded the time in each case. Fall time was obtained for each fruit as the average of three trials. For *Dimorphotheca* species, population averages were adjusted according to the population fruit morph ratio.

One assumption not tested here is that fall time is proportional to dispersal distance. This is a reasonable notion because lateral movement of a wind-dispersed diaspore in a breeze is a function of the height of release, the wind velocity and the settling velocity (a higher fall time corresponds to a lower settling velocity). A similar approach using fall time, settling velocity or rate of descent as proxy for dispersal distance has been used in other studies of wind-dispersed plants (Matlack, 1987; Andersen, 1992; Cody & Overton, 1996; Fresnillo & Ehlers, 2008). Our measures of fall time are also tightly correlated to measures of wing loading (the ratio of mass to surface area of the fruit; C. de Waal unpubl. data). Wing loading has often been shown to be an accurate surrogate for dispersal distance, with a low wing loading corresponding to a greater dispersal distance (Augspurger, 1986;

Augspurger & Franson, 1987; Matlack, 1987). Finally, our measures of fall time correspond to the range of descent rates recorded for other winged or finned fruit (e.g. samaras or fruit with a persistent calyx) reported in Matlack (1987).

Statistical analyses

All analyses were performed in the statistical package R version 3.0.0 (R Development Core Team, 2008). For each species, we assessed ability to self-fertilise in relation to range position by comparing pollination treatments in populations from range centres and range margins using generalised linear models with the function `glm`. The model included pollination treatment, range position and their interaction, except for *D. polyptera*, *O. microcarpum* and *U. calenduliflora*, for which we did not have both range positions. For these three species, only pollination treatment was included. For two species where we had sampled more than one range-edge and/or central population, data from populations in the same range position were pooled.

As fruit set data were over-dispersed (dispersion parameters 1.5 - 8), we used a quasi-poisson approach (Zuur *et al.*, 2009). Significance of effects was estimated by analysis of deviance in which terms were dropped from the model and quasi-F values were compared to the F distribution. The interaction term was dropped from a model also including the main effects. Each main effect was dropped from a model including both main effects, except for *D. polyptera*, *O. microcarpum* and *U. calenduliflora*. In these species pollination treatment was the only effect, so a model with the pollination treatment effect was compared to an intercept-only model. Contrasts were performed for pollination treatments and the range position-by-pollination treatment interaction, with hand self-pollination as the reference treatment.

We tested whether AF_X and fall time differed between central and range-edge populations across species with Wilcoxon's signed ranks tests. For *U. cakilefolia* and *G. tenuifolia*, where we had more than one range-edge and/or central population, we used the mean of population index values for each range position. Within each species, dispersal ability of range-edge versus central populations was compared using Welch t-tests.

We used a phylogenetic least squares (PGLS) analysis to assess the relationship between AF_X and fall time in relation to range position. The phylogeny used in PGLS was pruned from trees in Panero and Funk (2008) and Funk and Chan (2008). Within genera, relationships between species were left unresolved except in *Ursinia*, in which two sub-genera are recognised (Prassler,

1967; Swelankomo, 2008). As we did not have information on branch lengths these were all set to one, except for populations within species which were set to zero. We tested for phylogenetic signal in AF_X and fall time with Abouheif's C_{mean} tests (Abouheif, 1999; Münkemüller *et al.*, 2012) using the function `abouheif.moran` in the package `adephylo` with the function `proxTips` and the method `oriAbouheif` for the proximity matrix (Jombart & Dray, 2008). AF_X and fall time displayed phylogenetic structure (Abouheif's C_{mean} tests; $p \leq 0.002$). Consequently we used the function `corBrownian` in the package `ape` (Paradis *et al.*, 2013) to obtain the phylogenetic correlation structure, assuming a Brownian motion model of evolution, and the function `gls` in the `nlme` package (Pinheiro *et al.*, 2014) to run the PGLS regression. Fall time was entered as the dependent variable and AF_X , range position and AF_X *range position as effects. Although the variables do not have a bivariate normal distribution (Fig. 2.2), the residuals are nevertheless normally distributed. The residuals also show no patterns with respect to fitted values or predictors. Thus the assumptions of the analysis are met (Quinn & Keough, 2002). When AF_X was entered as the dependent variable, results were similar but assumptions were no longer met (J.G. Rodger, unpubl. results).

Results

Breeding system and dispersal traits within species

Pollination treatment significantly affected fruit set in all species except *Gazania tenuifolia*, *Osteospermum monstrosum*, *Ursinia anthemoides* and *U. nana* (Table 2.2; Table S2.3; Figs. S2.1-S2.4). AF_X values (Table S2.2) classify these four species as fully self-compatible. These species are also highly autonomously self-pollinating, as indicated by similar values for fruit set in hand self-pollination and autonomous self-pollination treatments (Figs. S2.2-2.4). Two species are partially self-compatible and capable of limited autonomous self-fertilisation (*O. amplexens* and *O. hyoseroides*). In contrast, seven species are strongly self-incompatible and have little or no ability to self-fertilise autonomously (*O. microcarpum*, *G. lichtensteinii*, *U. cakilefolia*, *U. calenduliflora*, *D. sinuata*, *D. pluvialis* and *D. polyptera*).

Across species, there were no consistent difference in fall time or AF_X between populations in range centres and range margins. Differences between range-edge and central populations were found within some species but these do not denote general patterns within species as only one population of each range position was sampled for most species. Only a single self-incompatible species, *D. pluvialis*, showed higher AF_X in the range-edge vs. the central population (Tables 2.2,

S2.3; Fig. S2.1a). For all other species the effect of pollination treatment did not differ between range-edge and central populations (Table 2.2). Fall time (dispersal ability) differed between range-edge and central populations for many of the species, but the direction of these differences was not consistent. Fall time was significantly higher in the central than in the range-edge populations for *D. sinuata* ($t_{18} = 3.20$, $P = 0.005$), *G. lichtensteinii* ($t_{38} = 2.50$, $P = 0.017$), *G. tenuifolia* ($t_{100} = 2.66$, $P = 0.009$), *O. hyoseroides* ($t_{57} = 4.84$, $p < 0.0001$) and *O. monstrosum* ($t_{62} = 5.51$, $p < 0.0001$). In contrast, significantly higher fall time values were observed in the range-edge compared to the central population of *O. amplexens* ($t_{58} = -3.60$, $p < 0.0001$) and *U. anthemoides* ($t_{54} = -6.38$, $p < 0.0001$). Populations from range centres and range margins did not differ significantly in fall time for *D. pluvialis* ($t_{16} = 1.65$, $P = 0.118$), *U. cakilefolia* ($t_{76} = -1.37$, $P = 0.175$) and *U. nana* ($t_{51} = 0.68$, $P = 0.50$).

Associations between breeding system, dispersal ability and range position across species

Across all species, range-edge populations did not differ significantly from central populations in either AF_X or fall time (Wilcoxon Signed Ranks tests; $V = 37$, $P = 0.375$ and $V = 36$, $P = 0.432$, respectively; Fig. 2.1).

AF_X was positively associated with fall time, taking phylogeny into account ($\beta = 0.61$, $t_{24} = 3.26$, $P = 0.003$; Fig. 2.2). The best model included AF_X only, and not range position or its interaction with AF_X ($\Delta AIC \geq 4.65$). When range position and its interaction with AF_X were included they were not significant ($p > 0.5$). The model including the hypothesised phylogeny was superior to the model with all phylogenetic relationships unresolved (equivalent to ordinary least squares regression ($\Delta AIC = 476$)). Nevertheless, the relationship between AF_X and fall time was also significant in this analysis ($\beta = 0.69$, $t_{24} = 2.90$, $P = 0.008$; Fig. 2.2).

Discussion

Our results show a significant positive relationship between selfing ability and dispersal, across multiple species, after controlling for phylogenetic structure (Fig. 2.2). This relationship and the bimodal distributions of values for fall time and autofertility (Fig. 2.2) suggest that the annual daisy flora of southern Africa comprises two discrete syndromes – more dispersive selfers and less dispersive outcrossers. These results are consistent with the good coloniser hypothesis and oppose the predictions of the Cheptou-Massol model (Cheptou & Massol, 2009; Massol & Cheptou,

2011a), which predict a dispersing, outcrossing strategy and a non-dispersing, selfing strategy. Contrary to the expectations derived from all models, (Pannell & Barrett, 1998; Sun & Cheptou, 2012), there were no associations between range position and dispersal or selfing ability (Fig. 2.1).

The assumptions of the Cheptou-Massol model (Cheptou & Massol, 2009; Massol & Cheptou, 2011a) that patches fluctuate in pollen limitation but do not fluctuate in suitability for occupation may not apply to our system of desert annual Asteraceae. Based on these assumptions, this model predicts that outcrossers are under selection to disperse to escape patches that become pollen limited. Selfers, on the other hand, do not experience pollen limitation and, as there is a cost to dispersal, they are selected not to disperse (Massol & Cheptou, 2011a). Fluctuations in pollen limitation in the Cheptou-Massol model are envisaged to occur through fluctuations in pollinator abundance (Cheptou & Massol, 2009). Such fluctuations are likely to be intense in plants specialised for pollination by one or a few pollinator species but our study species are Asteraceae, which typically have generalised pollinator systems involving several species of taxonomically diverse insects (Torres & Galetto, 2002). Such generalised plant species are buffered against fluctuations in abundance of particular pollinator species, so therefore are unlikely to be subject to substantial spatiotemporal variation in pollinator availability. However, arid systems such as ours are subject to high spatio-temporal variation in climatic conditions and disturbance regimes (Perry & Gonzalez-Andujar, 1993) so patches should fluctuate in suitability for occupation over time, selecting for the good coloniser syndrome. This scenario is consistent with the assumptions and results of modelling by Pannell and Barrett (1998).

There was no significant difference in selfing or dispersal ability between range-edge and central populations across our study species. Although there were differences in selfing and dispersal ability between the range-edge and central populations examined for certain species (Table 2.2, Fig. 2.1), we cannot draw general conclusions about effects of range position within species, as we only sampled one population of each range position for most species. There is thus no evidence that the correlation between selfing and dispersal ability across species is related to range position. This suggests that gradients of increased pollen limitation or reduced availability of suitable habitat patches from range centres to range margins (Pannell & Barrett, 1998; Sun & Cheptou, 2012) do not generally occur in this system. For species with generalised pollination systems, gradients of pollen limitation from central to range-edge populations are less likely than for plants with highly specialised and localised pollinators (Moeller, 2006; Sun & Cheptou, 2012). Even species with relatively specialised pollination systems do not necessarily have higher pollen limitation at range margins (Busch, 2005; Herlihy & Eckert, 2005). We also suggest that gradients

of decreased availability of suitable habitat from range centres to range margins are less likely to occur in arid systems, but that they should experience high spatiotemporal variation in habitat suitability throughout the range (Perry & Gonzalez-Andujar, 1993). Without such gradients, there is no reason to expect associations of dispersal and selfing ability with range position.

Biologists have only recently attempted to address the joint variation in both dispersal and selfing traits across species' geographical ranges (Darling *et al.*, 2008; Sun & Cheptou, 2012). Our multispecies study is, to our knowledge, the first empirical investigation of whether the evolution of breeding system and dispersal in response to range position is a general phenomenon. A detailed study of 34 populations of the dune plant *Abronia umbellata* revealed a positive association between selfing and dispersal ability, consistent with our results. However, unlike in our study, dispersal and selfing ability increased from range centres to range margins (Darling *et al.*, 2008).

The reason why some species in our system display the more dispersive, selfing syndrome and others the less dispersive, outcrossing syndrome remains to be determined. One potential explanation is that dispersive selfers occupy more stochastic habitats than less dispersive outcrossers. However, the species exhibiting these two syndromes do not differ obviously in the kind of habitat they occupy. It seems likely that the two syndromes are persistent strategies, with self-compatibility providing reproductive assurance to dispersal-prone individuals that are more likely to experience conditions of pollen limitation when they colonise new patches, and less dispersive outcrossers being better at persisting in patches. Another possibility, which we are currently investigating, is that the dispersal-selfing association arises because of dispersal consequences which are unrelated to the colonisation of new sites. For example, whereas species with limited dispersal likely exhibit aggregated distributions, individuals of dispersive species may be more widely scattered. Scattered individuals are in turn more likely to experience pollen limitation because of distance from mates, competition for pollinators and interspecific pollen transfer. Selfing would provide reproductive assurance in this context, resulting in the association between dispersal and selfing ability which we detected.

Conclusions

We find no support for the model predictions of Cheptou and Massol (2009), Massol and Cheptou (2011a) and Sun and Cheptou (2012). Instead, our finding of a positive association between autofertility and dispersal ability is consistent with Baker's Law and the good coloniser hypothesis (Baker, 1955, 1967; Pannell & Barrett, 1998). We argue that in generalist-pollinated desert annuals,

pollen limitation is likely to be independent of range position. Hence associations between range position and dispersal and/or selfing ability are not to be expected. However, recolonisation following local extinction could favour dispersive selfers throughout the range. Regardless of the underlying mechanism, our findings suggest that in southern African daisies, selfing ability has evolved in tandem with dispersal ability, most likely because self-compatibility offers reproductive assurance to dispersal-prone individuals that are more likely to experience conditions of pollen limitation, regardless of range position.

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Table 2.1. Prevalent and often conflicting hypotheses predict different associations between dispersal and selfing ability*, as well as varying effects of range position on these traits. Examples of theoretical and empirical references that are consistent with each set of predictions are provided. Note that this is not intended to be a complete review of the literature related to this subject.

| Prediction | Reason for prediction | Examples of theoretical references | Examples of empirical references |
|---|---|--|--|
| <i>Relationship between dispersal and selfing ability:</i> | | | |
| Positively correlated | “Good coloniser syndrome” – both selfing ability and dispersal are advantageous when colonisation ability is favoured | <i>Selfing ability as reproductive assurance mechanism:</i> (Pannell & Barrett, 1998; Dornier <i>et al.</i> , 2008) | <i>Benefits of selfing ability during colonisation:</i> (Baker, 1955, 1967; McMullen, 1987; Bernardello <i>et al.</i> , 2001; van Kleunen <i>et al.</i> , 2008) <i>Benefits of dispersal during colonisation:</i> (Richardson <i>et al.</i> , 1994) (Stebbins, 1957; Randle <i>et al.</i> , 2009) |
| Negatively correlated | Avoidance of recombination to preserve favourable genotypes in the new habitat Under conditions of pollination heterogeneity, dispersal benefits outcrossers but not selfers Inbreeding avoidance drives the evolution of dispersal | † (Cheptou & Massol, 2009; Massol & Cheptou, 2011a) (See references in Ronce, 2007; and Auld & Rubio de Casas, 2012) | (Bawa, 1980; Givnish, 1980; Primack, 1987) (Cheptou <i>et al.</i> , 2001; Szulkin & Sheldon, 2008; and other references in Auld & Rubio de Casas, 2012) |
| | Selfing and reduced dispersal contribute to avoidance of outbreeding depression and fosters local adaptation | † | (See references in Auld & Rubio de Casas, 2012) |
| <i>Effect of range position on breeding system:</i> | | | |
| Higher selfing ability at margins | Reproductive assurance in marginal habitats | (Pannell & Barrett, 1998) | (Barrett <i>et al.</i> , 1989; Busch, 2005; Moeller & Geber, 2005; Michalski & Durka, 2007) |
| <i>Effect of range position on dispersal:</i> | | | |
| High dispersal at margins | Expanding range margin, e.g. during invasion | (Travis & Dytham, 2002; Hughes <i>et al.</i> , 2007) | (Phillips <i>et al.</i> , 2006; Hughes <i>et al.</i> , 2007) |
| Low dispersal at margins | High turnover of populations High cost of dispersal (e.g. islands, recent fragmentation) | (McPeck & Holt, 1992; Dytham, 2009) (McPeck & Holt, 1992; Dytham, 2009) | (Darling <i>et al.</i> , 2008) (Cody & Overton, 1996; Cheptou <i>et al.</i> , 2008) |

Effect of range position on joint evolution of selfing ability and dispersal:

| | | | |
|--|--|--|---------------------------------|
| Selfing ability + dispersal at margins | Reproductive assurance/metapopulation dynamics | (Pannell & Barrett, 1998) | (Darling <i>et al.</i> , 2008) |
| Outcrossing + dispersal at range centre / Selfing ability + low dispersal at margins | Gradients of pollination limitation, habitat availability and inbreeding | (Sun & Cheptou, 2012) | † |
| Selfing ability + low dispersal at margins | Facilitation of local adaptation | (Holt & Gomulkiewicz, 1997; Kirkpatrick & Barton, 1997; Eva Kisdi, 2002) | (See references in Levin, 2010) |

*For the purposes of this table we did not distinguish between selfing ability and self-fertilisation, although most of these hypotheses deal explicitly with one or the other. We assume that selection for self-fertilisation will entail selection for selfing ability (e.g. self-compatibility, pollinator independence).

† Lack of either empirical or theoretical studies to support the particular prediction.

Table 2.2. Results of generalised linear models for effects of pollination treatment, range position and their interaction on fruit set in controlled pollination experiments in thirteen annual Asteraceae species. Full results are available in Table S2.3.

| Species | Pollination treatment | Range position | Pollination*Range position |
|--------------------------|-----------------------|----------------|----------------------------|
| <i>D. pluvialis</i> | X > S, A *** | ns | * |
| <i>D. polyptera</i> † | X > S, A *** | - | - |
| <i>D. sinuata</i> | X > S, A *** | C > M *** | ns |
| <i>G. lichtensteinii</i> | X > S, A *** | ns | ns |
| <i>G. tenuifolia</i> | ns | ns | ns |
| <i>O. amplexans</i> | X > S, A *** | ns | ns |
| <i>O. hyoseroides</i> | X > S, A *** | C > M *** | ns |
| <i>O. microcarpum</i> †‡ | * | - | - |
| <i>O. monstrosum</i> | ns | ns | ns |
| <i>U. anthemoides</i> | ns | ns | ns |
| <i>U. calenduliflora</i> | X > S, A ** | - | - |
| <i>U. cakilefolia</i> | X > S, A *** | C > M * | ns |
| <i>U. nana</i> | ns | C > M ** | ns |

X = hand cross-pollination, S = hand self-pollination, A = autonomous self-pollination, C = central populations,

M = range-edge populations

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns = not significant

† Population(s) from only one range position sampled

‡ The main effect of pollination treatment was significant, but the contrasts between treatment pairs were all non-significant

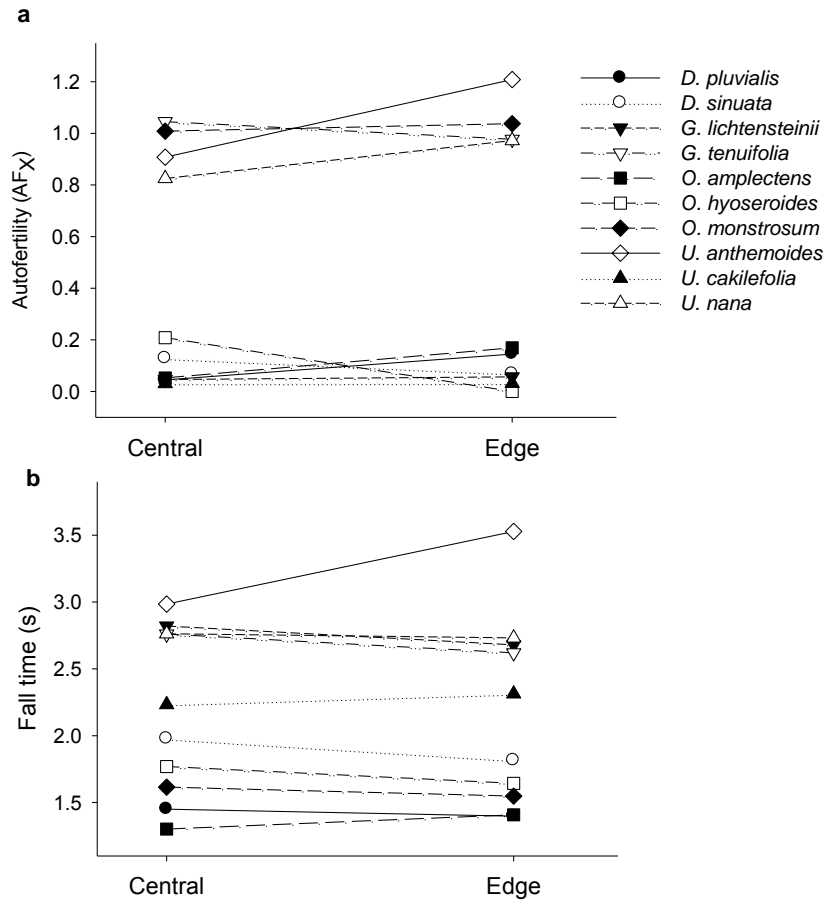


Fig. 2.1. (a) AF_x, an index of autofertility, and (b) fall time, a measure of dispersal ability, for range-edge and central populations of ten annual Asteraceae species.

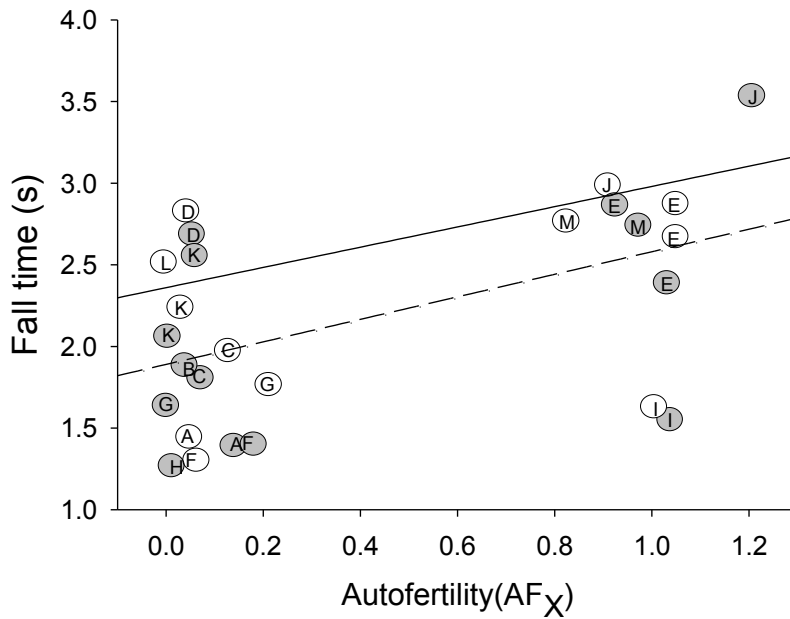


Fig. 2.2. The association between fall time, a measure of dispersal ability, and index of autofertility (AF_X) for populations of thirteen annual Asteraceae species. The regression model taking hypothesised phylogenetic relationships into account (solid line; see text) is superior to a model assuming a star phylogeny (dashed line). Clear circles with large letters indicate central populations and grey circles with small letters indicate range-edge populations. A = *Dimorphotheca pluvialis*, B = *D. polyptera*, C = *D. sinuata*, D = *Gazania lichtensteinii*, E = *G. tenuifolia*, F = *Osteospermum amplexens*, G = *O. hyoseroides*, H = *O. microcarpum*, I = *O. monstrosum*, J = *Ursinia anthemoides*, K = *U. cakilefolia*, L = *U. calenduliflora*, M = *U. nana*.

Chapter 3

Relative density and dispersion pattern of two southern African Asteraceae affect fecundity through heterospecific interference and mate availability, not pollinator visitation rate

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Abstract

Since co-flowering plants often share pollinators, their fecundity is likely affected by pollen transfer within and among plant species. Changes in pollinator visitation rates (e.g. through facilitation or competition for pollinators) are usually thought to exert the predominant influence on plant fecundity. However, the transfer of conspecific relative to heterospecific pollen between individuals may also play an important role. Indeed the relative importance of these determinants of fecundity is expected to depend on the density, relative abundance and spatial arrangement of con- and heterospecifics. We investigated the effects of con- and heterospecific density and spatial distribution pattern on pollinator visitation and plant fecundity within and between two annual, self-incompatible co-flowering species (*Dimorphotheca pinnata* and *Ursinia cakilefolia* (Asteraceae)) by manipulating their relative abundance, overall patch density, and dispersion patterns in experimental arrays in Namaqualand, South Africa. We quantified pollinator visitation rates and fruit set in arrays of varying density and aggregation. This enabled us to determine which mechanism(s) were driving variation of fecundity, particularly through their influence on visitation rates, mate availability and heterospecific pollen interference. To test whether autogamy offers reproductive assurance when individuals are scattered amongst a dense population of heterospecifics, we included an autogamous species (*U. anthemoides*) in a separate experiment. We found that increased fecundity with increasing conspecific density was not the result of higher visitation rates, but rather increased mate availability. Furthermore, increased spatial aggregation of conspecifics at low density significantly increased fecundity through reduced heterospecific interference. In contrast to results for self-incompatible species, fruit set in *U. anthemoides* was consistently high and unaffected by scattered distribution patterns. This suggests that autogamy offers reproductive assurance when mates are limited and the potential for interspecific pollen transfer (IPT) is high. In this study of annual daisies, variation in fruit set is primarily driven by factors that affect the transfer of conspecific relative to heterospecific pollen, independent of pollinator visitation rate. Our findings demonstrate that mate limitation and IPT negatively affect fruit set and that these effects can be mitigated by intraspecific aggregation and the ability to autonomously self-pollinate.

Introduction

An estimated 87.5 % of flowering plants rely on pollinators to reproduce (Ollerton *et al.*, 2011) and pollinators are often shared among co-flowering plants (Rathcke, 1983; Mitchell *et al.*, 2009). Consequently the identity, morphology and spatial arrangement of neighbouring plants may influence the fecundity of co-flowering individuals. The effects of both conspecific and heterospecific plants on the fecundity of their neighbours are determined by factors such as pollinator foraging patterns (e.g. Morgan *et al.*, 2005; Lázaro & Totland, 2010) and the relative attractiveness of flowering species to pollinators (Hanoteaux *et al.*, 2013). In turn, these pollinator-mediated interactions may affect the evolution of plant mating systems (Fishman & Wyatt, 1999; Kariyat *et al.*, 2013).

Pollinator-mediated interactions between plant species can affect fecundity of focal species positively or negatively through mechanisms dependent on their density, relative abundance and spatial dispersion patterns (the arrangement of individuals within the community, i.e. clumped or uniform). The predicted effects of these mechanisms on fruit set are traditionally thought to reflect changes in pollinator visitation rates to individuals. For example, aggregations of con- and heterospecific co-flowering plants may facilitate increased pollinator visitation to all individuals by increasing the floral display (Rathcke, 1983; Moeller, 2004). Facilitation may also occur within species, where pollen removal and deposition increases with density of neighbouring conspecifics (e.g. Duffy & Stout, 2011). However, the latter mechanism may also act independently of pollinator visitation rate, i.e. increased mate availability (conspecific density) may result in higher seed set because of a higher probability of conspecific pollen transfer, even if visitation rates or pollinator abundance do not increase (Kunin, 1993; Moeller, 2004).

Increasing plant density (the number of flowering individuals per unit area) is predicted to facilitate an increase in pollinator visitation rate per flower until competition for pollinators occurs when pollinator visits become saturated (e.g. Rathcke, 1983; Essenberg, 2012). Consequently, reduced intraspecific competition for pollinators may increase fecundity at lower conspecific density (Wirth *et al.*, 2011). On the other hand, individuals of less attractive species (in terms of morphology and/or reward) or species at low relative abundance may be unable to compete with co-flowering species for pollinator attraction

(Feinsinger *et al.*, 1991; Hanoteaux *et al.*, 2013). Such interspecific competition for pollination may drive divergence in floral traits between species and even drive shifts between specialist and generalist pollination strategies (Sargent & Otto, 2006). Alternatively, traits associated with self-pollination may be selected in weaker competitors (Wyatt, 1986).

Reduced conspecific density may give rise to component Allee effects, defined as a reduction in any component of individual fitness (e.g. number of matings, fecundity, etc.) with decreasing density or population size (Stephens *et al.*, 1999). Mate-finding, a common mechanism that may generate component Allee effects (Gascoigne *et al.*, 2009), is hampered in self-incompatible plants by inadequate pollen receipt at low densities (pollen limitation; Davis *et al.*, 2004). For example, animal pollinators are less likely to discover, or forage from more isolated, sparser, or smaller patches of plants (Ågren, 1996; Groom, 1998). Furthermore, when individuals occur at very low density, or are isolated from a source of conspecific pollen, pollinators may carry insufficient amounts of suitable pollen, even if visitation per plant does not decline (Duncan *et al.*, 2004; Brys *et al.*, 2007; Rodger *et al.*, 2013).

Fecundity of an individual may also be affected by negative interactions with its neighbours via interspecific pollen transfer (IPT), i.e. heterospecific pollen interference. The presence of heterospecific pollen may reduce the fertilisation success of conspecific pollen, and pollen loss to heterospecific flowers reduces the amount of pollen transferred between conspecific flowers (reviewed in Morales & Traveset, 2008; Ashman & Arceo-Gómez, 2013). The negative effects of IPT may be particularly important for individuals at low density and low relative abundance. Visits to rare flowers are likely to be followed by visits to heterospecifics, and pollinators arriving at rare flowers are likely to carry more heterospecific pollen grains (Palmer *et al.*, 2003). Consequently, pollination success can be reduced at low conspecific density due to IPT, giving rise to a pattern akin to a mate-finding Allee effect (Gascoigne *et al.*, 2009). In plant species, several studies have demonstrated how the presence of co-flowering heterospecifics can lower fecundity through IPT (e.g. Feinsinger *et al.*, 1991; Jakobsson *et al.*, 2009; Matsumoto *et al.*, 2010), but to our knowledge none has explicitly explored the possibility that IPT may contribute to component Allee effects generated under conditions of low density or low relative abundance.

The strength of these interactions will, to a large extent, depend on the abundance of con- and heterospecific co-flowering plants (Rathcke, 1983) and on the spatial arrangement, or dispersion, of individuals within the community (Stoll & Prati, 2001). For example, competitive interactions can increase with a decline in absolute density of both conspecifics and heterospecifics, because there are not sufficient numbers of plants to attract enough pollinators (Caruso, 2002). Alternatively, competition can increase at high plant density, because there are too few pollinators available to pollinate individuals in dense aggregations (Essenberg, 2012; Ward *et al.*, 2013). The frequency of IPT should decrease with a decrease in relative density of heterospecifics (e.g. Feinsinger *et al.*, 1991; Stout *et al.*, 1998).

Similarly, aggregated (clumped) dispersion patterns reduce the extent of heterospecific pollen movement (Campbell, 1986; Feinsinger *et al.*, 1986) while retaining the benefits of joint attraction of pollinators (Moeller, 2004). While several studies have demonstrated that density and dispersion affect pollinator visitation rates and/or fecundity of co-flowering individuals (e.g. Duffy & Stout, 2011) as well as the intensity of interspecific competition for pollinators (Hanoteaux *et al.*, 2013), few have attempted to tease apart the confounding mechanisms (i.e. pollinator visitation, mate availability and heterospecific pollen transfer) which underlie these effects (but see Feinsinger *et al.*, 1991; Kunin, 1993; Rodger *et al.*, 2013). Here, we report results of arrays set up to experimentally determine the mechanisms responsible for density (relative and absolute) and dispersion dependent fecundity of two Namaqualand daisies in South Africa.

The Namaqualand region of southern Africa's Succulent Karoo biome is renowned for its spectacular displays of spring annuals. Following the winter rains, multiple species germinate and flower in the relatively short growing season, often forming dense co-flowering communities, particularly in disturbed sites (Cowling *et al.*, 1999). These communities consist predominantly of various native Asteraceae species and are often dominated by a single species (usually *Ursinia* or *Dimorphotheca* species) with other species scattered in between at lower densities. It is therefore possible that individuals of these relatively sparsely distributed species may suffer greater fecundity costs through interspecific competition, low mate availability and/or IPT than individuals of relatively densely distributed species.

Here we explore positive and negative interactions within and between co-flowering species. We aimed to tease apart the mechanisms by which density and dispersion affect fecundity through their influence on 1) pollinator visitation rates (intra- and interspecific facilitation and competition for visits), 2) mate availability, and 3) heterospecific interference. To do this, we manipulated relative abundance, overall patch density, and dispersion patterns in experimental arrays with two self-incompatible, annual Asteraceae species from Namaqualand, South Africa (Figs. 3.1 and 3.2). An autogamous species was included in the final array. Specifically, we ask: 1) What are the effects of absolute density, relative abundance, and dispersion pattern on pollinator visitation rates to each co-flowering species?; 2) What are the effects of these factors on plant fecundity (fruit set)?; 3) Do changes in pollinator visitation rates, if present, explain variation in fruit set in relation to density and dispersion patterns, according to predictions derived from the aforementioned mechanisms (outlined in Fig. 3.3)?; 4) Does self-compatibility offer reproductive assurance to scattered individuals at low density?

Materials and Methods

Study species

Three spring-flowering annual Asteraceae species native to the Namaqualand region of South Africa were used in our experimental arrays: *Dimorphotheca pinnata* (Thunb.) Harv., *Ursinia cakilefolia* DC. and *U. anthemoides* (L.) Poir. (Fig. 3.2). *Dimorphotheca pinnata* and *U. cakilefolia* frequently dominate spring displays in communities across Namaqualand (Van Rooyen 1999) and populations are often dense, with 39.9 ± 45.7 SD (maximum = 155) inflorescences per m² for *D. pinnata* and 17.7 ± 14.4 (maximum = 98) for *U. cakilefolia* (A.G. Ellis, unpubl. data). In our study area both produce inflorescences with bright orange rays and offer nectar and pollen as rewards to visiting pollinators. In addition, both species tend to exhibit aggregated dispersion patterns resulting in a patchwork of local clumps with high density and relative abundance of a particular species. Although all three species coexist in the study area, *U. anthemoides* individuals are frequently scattered among other species in these communities and produce much smaller inflorescences with salmon-coloured rays (Fig. 3.2; C. de Waal pers. obs.). The pollinator community in the region is dominated by a diverse

assortment of insects with generalist visitation tendencies; predominated by bees, bee-flies and monkey-beetles (Struck, 1994; Ellis & Johnson, 2009; De Jager & Ellis, 2014). These insects visit a wide range of plant species, characterised by open flowers and inflorescences (e.g. Asteraceae and Mesembryanthemaceae), which make their rewards accessible to a wide range of insects. *Megapalpus capensis* (Bombyliidae), a key pollinator of orange daisies, does not exhibit floral constancy (Ellis & Johnson, 2012). Despite the rich supply of floral reward during the flowering season, some authors have suggested that the abundance of flower-visiting insects is relatively low (Struck, 1994; Esler, 1999).

To determine the breeding system of *D. pinnata*, we conducted controlled pollination experiments, following the methods described in De Waal *et al.* (2014). We conducted these experiments on individuals from the same *D. pinnata* population used in our experimental arrays (Kamieskroon; 30° 12' 19.96" S 17° 56' 10.59" E, 757 m). An index of self-incompatibility (ISI), calculated as $1 - \text{hand self-pollination} / \text{hand cross-pollination}$ (Zapata & Arroyo, 1978), indicated that this population is self-incompatible (ISI = 0.97). Sample sizes were 16 inflorescences for the hand self-pollination treatment and 13 inflorescences for the hand cross-pollination treatment. The breeding systems of *U. cakilefolia* (self-incompatible; ISI \approx 0.96) and *U. anthemoides* (self-compatible and autogamous; ISI \approx 0.03) were previously determined through controlled pollination experiments (De Waal *et al.*, 2014).

Experimental arrays

Experimental arrays were set up on the premises of the South African National Parks offices in Kamieskroon, Northern Cape Province. Plants with buds were collected from populations of our study species in the vicinity of Kamieskroon. Plants were transplanted into 18 cm diameter pots – three plants of the same species per pot – with soil from the same site where they were collected.

We experimentally manipulated various naturally occurring plant dispersion/density scenarios in arrays of potted plants, approx. 1.5 m \times 1.5 m in extent (Fig. 3.2). Each experimental block (five in total) consisted of six different treatment arrays. Arrays consisted of either 64 or eight pots depending on the treatment (see below; Figs. 3.1 and 3.2), with three conspecific plants per pot. The experimental design consisted of: 1) a high density background of *D. pinnata* (filled circles in Fig.3.1) with *U. cakilefolia* (open circles in

Fig.3.1) widely dispersed among the background pots. This represented the high density (HD) treatment for *D. pinnata* and low density dispersed (LDD) treatment for *U. cakilefolia*; 2) a high density background of *D. pinnata* with *U. cakilefolia* arranged in an aggregated/clumped pattern in the centre of the array, representing the HD treatment for *D. pinnata* and low density clumped (LDC) treatment for *U. cakilefolia*; 3) the reciprocal arrangement of treatment 1, i.e. HD treatment for *U. cakilefolia* and LDD treatment for *D. pinnata*; 4) the reciprocal arrangement of treatment 2, i.e. HD treatment for *U. cakilefolia* and LDC treatment for *D. pinnata*; 5) an array where both self-incompatible species occur at low density (LD treatment for both species); 6) a high density background of *D. pinnata* with *U. anthemoides* (the autogamous species; triangles in Fig. 3.1) at low density and arranged in a dispersed pattern (LDD treatment for *U. anthemoides*). Focal plants in the HD treatments were adjacent to heterospecific plants in the LDD and LDC treatments (Fig. 3.1) to avoid edge effects in the arrays, and to ensure that these treatments differed only in conspecific abundance and not proximity to heterospecific inflorescences.

The six arrays within each experimental block were spaced 5 m apart, and the five experimental blocks were separated from one another by at least 20 m. Although *D. sinuata*, with inflorescences morphologically similar to *D. pinnata*, occurred on and around the premises where the experiment was performed, we ensured that co-flowering individuals did not interfere with our experiment by removing inflorescences in close proximity to our experimental plants. All experiments were performed within a 100×100m area. We repeated the full experiment twice during the spring flowering season. The first run of the experiment (Experiment 1) was conducted at the end of August 2013, and the second run (Experiment 2) was conducted during mid-September 2013. To increase the magnitude of an interference effect (if present) in Experiment 2, pots in the LDD treatment were spaced even further apart toward the corners of the array, with four pots of the background species in between pairs of focal pots (instead of two pots as in Experiment 1).

To maintain an even density of plants in the low density treatments (LDD, LDC and LD), only one of the three plants in each of the four focal pots was allowed to flower and to produce one inflorescence. This developing focal inflorescence on each of these plants was tagged with coloured string. Similarly, one developing focal inflorescence in each of four pots of the high density background species (HD treatment) adjacent to the LDD/LDC pots was tagged (grey circles in Fig. 3.1). Focal inflorescences were left to mature on the plants at

the end of each experiment and infructescences were subsequently collected, i.e. eight infructescences per array (four per species). Following the approach of De Jager & Ellis (2014) and De Waal *et al.* (2014), the number of fruits per infructescence was counted, with clearly swollen ovaries regarded as fruit. In addition, we counted the number of unfertilised female-fertile florets (florets with small, unenlarged ovules) per infructescence under a dissecting microscope.

Pollinator observations

To determine whether inflorescence density and/or dispersion in experimental arrays affected pollinator visitation rates, we conducted observations of pollinator visits to each species. Each array was observed for a five minute interval once every day for four to six days for Experiment 1 (26 August – 5 September 2013), and over two days for Experiment 2 (16 and 17 September 2013). We opted for short (five minute) observation intervals so that all arrays could be observed through the course of one day. In total, observations occurred over 155 separate five minute periods. Pollinator observations were performed only when all four focal inflorescences in the low density treatment of a particular array were flowering. Each day, observations were conducted when inflorescences were fully open (as inflorescences open and close each day) and pollinators were active, approximately between 10:45 am and 4:15 pm. Before each observation interval, the number of open inflorescences for the background species in high density arrays (HD treatment) was counted. The number of visits per inflorescence per five minute observation period was used as a measure of visitation rate. All insects that made contact with the plants' reproductive organs, whether they were stationary during the observation period, moving between plants or entering/leaving the array, were recorded as visitors and identified to morphospecies level.

Treatment contrasts for elucidating underlying mechanisms

Our experimental design allowed us to determine which mechanisms drive variation in fecundity under different dispersion patterns and relative densities (illustrated in Fig. 3.3). If variation in fecundity reflects the effects of density and dispersion on pollinator attraction (i.e. facilitation or competition for visits), we would expect fruit set across array treatments to track patterns of pollinator visitation. However, if density and dispersion affect plant fecundity through their influence on the quality of pollen loads arriving on stigmas (i.e. mate

availability or interference) we do not expect fruit set patterns to be coupled with patterns of pollinator visitation across treatments. The contrasts outlined in Fig. 3.3 reflect treatment comparisons which are least likely to be confounded by mechanisms other than the one under consideration, resulting in predictions for combined pollinator visitation and fruit set patterns unique to each underlying mechanism.

To test for intraspecific effects of competition, facilitation and mate availability, we used contrasts between HD and LD treatments because density of the focal species was the only parameter that varied between these treatments (although we acknowledge that plants in the LD treatment might have experienced some heterospecific interference). To test for interspecific effects of facilitation and pollinator limitation, we used contrasts between the LD and LDD/LDC treatments, because these treatments differ in the density of heterospecifics but not conspecifics. To examine whether plant species that occur at low density amongst dense aggregations of heterospecifics are at a disadvantage because pollinators are attracted to the common species, we compared visitation rates to plants in the HD treatment to those in the LDD and LDC treatments, because these differ in the abundance of the focal species but not overall array density. To test for the presence of an interference effect, we used contrasts between the LDC and LDD treatments because these treatments differed only in the dispersion pattern of the focal species, whereas array density and relative abundance of the two species remained the same.

Statistical analyses

Pollinator visitation:

All analyses were performed in R version 3.0.2 (R Core Team, 2013). Overlap in pollinators between *D. pinnata* and *U. cakilifolia* was explored by comparing visitation rates (number of visits per inflorescence per five minute observation period) of the predominant insect visitors, *Megapalpus capensis* (Bombyliidae) and monkey beetles (Scarabaeidae), across daisy species using Mann Whitney U tests with the `wilcox.test` function. The observed and expected frequencies of intra- and interspecific transitions on our arrays were compared with a Pearson's Chi-squared test using the `chisq.test` function.

To determine whether pollinator visitation varied between daisy species and the first and second run of the experiment, we compared the number of pollinator visits per five

minute observation period to *D. pinnata* and *U. cakilefolia* in the high density (HD) treatments using a generalized linear model. This was done in the `glm.nb` function in the MASS package (Venables & Ripley, 2002) using a negative binomial distribution and a log link function. Plant species, experiment and the species \times experiment interaction were included as explanatory variables, with $\log(\text{number of inflorescences})$ as an offset variable to account for variation in open inflorescences in the HD treatments. Significance of predictors was determined using likelihood ratio tests to compare the full model with reduced models after single term deletion in the `anova` function. To compare levels of the interaction effect between species and experiment, the model was run using an interaction variable (created with the function `interaction`) as predictor, followed by Tukey's contrasts using the `glht` function in the package `multcomp` (Hothorn *et al.*, 2008). In this analysis as well as other analyses of pollinator visitation rates and fruit set (see below), we pooled data from the two different HD treatments (Fig. 3.1) where only the dispersion pattern of the low density species differed.

To examine the effects of our array treatments on total pollinator visitation rates, we used generalised linear mixed models (GLMMs) in the package `lme4` (Bates *et al.*, 2013) for each species-by-experiment combination. The response variable was the number of pollinator visits in each five minute observation period, with $\log(\text{number of inflorescences})$ as an offset variable. The models included treatment as a fixed factor (corresponding to the treatment factor used in fruit set analyses), and block as a random factor. To account for potential variation in visitation rates throughout the day, we incorporated the time of the start of each observation period as an additional fixed categorical factor with three categories: morning (observations conducted between 10:30 am – 12:30 pm), midday (12:31 pm – 2:30 pm) and afternoon (2:31 pm – 4:30 pm).

Models were selected following inspection of overdispersion parameters (ratio of residual scaled deviance to the residual degrees of freedom), visual inspection of residuals, and finally comparisons of Akaike Information Criterion (AIC) values. Accounting for zero-inflation did not improve models in any of the cases. The significance of fixed effects was examined by conducting likelihood ratio tests in which a model with only one of the two fixed effects was compared to the full model using the `anova` function.

Based on model selection, visitation rates to *D. pinnata* (Experiment 1) and *U. cakilefolia* (Experiment 1 and 2) were analysed using a negative binomial GLMM and a log link function in the `glmer.nb` function. For *D. pinnata* in Experiment 2, two treatment categories (LD and LDC) as well as one time category (morning) had zero visitations which led to numerical problems in the analysis. Consequently, we randomly assigned a single visit to one observation period in each treatment category. Visitation rates in this case were analysed using a GLMM with a poisson distribution and log link function with the `glmer` function. Tukey's contrasts were used to assess predicted array contrasts (Fig. 3.3), using the `glht` function in the package `multcomp` (Hothorn *et al.*, 2008). Fitted values of the number of visits per five minute interval were divided by the number of inflorescences to obtain the predicted estimates of visitation rate.

To test for an additional signal of an interference effect, we compared pollinator visitation rates to *D. pinnata* and *U. cakilefolia* plants in the LDD treatment in Experiment 1 with plants in Experiment 2, in which we increased the distance (and number of heterospecifics) between focal inflorescences. Visitation rates were analysed using the same approach as before: a GLM with a negative binomial distribution and a log link function using the `glm.nb` function in the package `MASS` (Venables & Ripley, 2002). Plant species, experiment and the species \times experiment interaction were included as explanatory variables. However, the interaction effect was not significant and therefore the final model included only effects of species and experiment.

Fruit set:

To assess the effect of our experimental array treatments on the fecundity of *D. pinnata* and *U. cakilefolia*, we again analysed each species \times experiment combination separately, using GLMMs with a binomial distribution using `glmer` in the package `lme4` (Bates *et al.*, 2013), because the species \times experiment interaction was significant in overall analyses. Fruit set was analysed as the total number of fruits out of the total number of female-fertile florets. The model included treatment as a fixed effect, and block as random (intercept-only) factor. Significance of the treatment effect was estimated by comparing a model in which treatment was dropped to the full model, using the function `anova`. A Tukey's test for post hoc multiple contrasts was conducted using `glht` in the package `multcomp` (Hothorn *et al.*, 2008) to establish the existence of predicted inequalities in fruit set (Fig. 3.3).

To assess whether the ability to self-fertilise autonomously ensures fecundity in conditions of low density and high heterospecific interference, we compared fruit set of the autogamous *U. anthemoides* and the self-incompatible *U. cakilefolia* and *D. pinnata* for focal plants in the LDD treatments in Experiment 1 vs. Experiment 2. This analysis was also performed with a GLMM and a binomial distribution using `glmer` (Bates *et al.*, 2013). The fruit set response variable was calculated in the same way as described above. Species (*U. anthemoides*, *U. cakilefolia* or *D. pinnata*), experiment (1 or 2) and the species \times experiment interaction were entered as fixed effects and block as random factor. Significance of the interaction effect and the two fixed effects was evaluated as described above. To compare levels of the interaction term we created an interaction variable (using the function `interaction`), ran the full model with this as predictor variable, and performed Tukey's contrasts using `glht` in the package `multcomp` (Hothorn *et al.*, 2008).

Results

Pollinator observations

Seventeen different insect morphospecies visited plants in our arrays during the observation periods across both experiments. The majority of recorded pollinator visits were by the bee fly *Megapalpus capensis* (Bombyliidae; 25.8 %) and various species of monkey beetles (Scarabaeidae; 58.9 %). Other visitors included horse flies (Tabanidae), blister beetles (Meloidae), *Corsomyza* (Bombyliidae), wasps (Hymenoptera) and biting midges (Ceratopogonidae). In total, we observed 516 visits by 316 pollinators during a total of 775 minutes of observation time. There was some overlap in pollinators between our study species: eight of the 17 morphospecies (47 % of recorded pollinator species) visited both *U. cakilefolia* and *D. pinnata* inflorescences in our arrays. In addition, we recorded 195 transitions between inflorescences, of which 10 (5.1 %) were interspecific. The observed number of intra- and interspecific transitions was too low for meaningful analyses. However, under random visitation (i.e. no preference of pollinators for either species) the expected frequencies of intraspecific (92.4%) and interspecific (7.6%) transitions on our arrays did not differ significantly from the observed intraspecific (94.9%) and interspecific (5.1%) transitions ($X^2 = 1.70$, $df = 1$, $P = 0.193$). *Dimorphotheca pinnata* was visited more

frequently by *Megapalpus capensis* (Mann-Whitney U test; $W = 12891.5$, $P = 0.028$) and *U. cakilefolia* by monkey beetles ($W = 7046.5$, $P < 0.001$).

The mean number (\pm SE) of inflorescences flowering per array in the HD treatments was 106.88 ± 3.19 and 70.5 ± 3.19 for *D. pinnata* in Experiments 1 and 2, respectively, and 93.2 ± 2.55 and 121.05 ± 4.02 for *U. cakilefolia* in Experiments 1 and 2, respectively. Total pollinator visitation rates for all taxa did not differ significantly between Experiments 1 and 2 (Fig. 3.4; likelihood ratio test, $X^2 = 0.47$, $df = 1$, $P = 0.494$). Instead we found a significant effect of plant species ($X^2 = 6.690$, $df = 1$, $P = 0.010$) and a significant interaction between species and experiment ($X^2 = 8.46$, $df = 1$, $P = 0.004$), where visitation rates were significantly higher in Experiment 1 than Experiment 2 for *D. pinnata* ($z = -2.77$, $P = 0.027$), but not for *U. cakilefolia* ($z = 1.17$, $P = 0.640$). In addition, visitation rates to *U. cakilefolia* were significantly higher than to *D. pinnata* in Experiment 2 ($z = 3.87$, $P < 0.001$), but not in Experiment 1 ($z = 0.83$, $P = 0.836$).

For *D. pinnata* in Experiment 1 (Fig. 3.4a) visitation rates did not differ significantly between time categories (likelihood ratio test, $X^2 = 1.38$, $df = 2$, $P = 0.619$) or treatments ($X^2 = 1.38$, $df = 3$, $P = 0.711$). In contrast, in Experiment 2 (Fig. 3.4b), treatment ($X^2 = 20.33$, $df = 3$, $P < 0.001$) and time category ($X^2 = 13.18$, $df = 2$, $P = 0.001$) significantly affected total pollinator visitation rate. For *U. cakilefolia* in Experiment 1 and Experiment 2 (Fig. 3.4c and Fig. 3.4d), treatment (Exp. 1: $X^2 = 38.82$, $df = 3$, $P < 0.001$; Exp. 2: $X^2 = 11.56$, $df = 3$, $P = 0.009$) and time category (Exp. 1: $X^2 = 15.54$, $df = 2$, $P < 0.001$; Exp. 2: $X^2 = 10.24$, $df = 2$, $P = 0.006$) significantly affected visitation rates. In *D. pinnata* (Experiment 2) and *U. cakilefolia* (Experiments 1 and 2), visitation rates to inflorescences in the HD treatment were significantly lower than to inflorescences in the LD treatment (Tukey's contrasts, $P < 0.05$), supporting our prediction for intraspecific competition for pollinators (Table 3.1). In *D. pinnata* (Experiment 2), visitation rates were higher during midday than in the morning ($P = 0.032$), but not different from the afternoon ($P > 0.05$). In *U. cakilefolia* (Experiments 1 and 2), visitation rates were higher in the afternoon compared to the morning ($P < 0.001$) and midday periods ($P \leq 0.007$).

No pollinator visits were observed to *U. anthemoides* inflorescences in either experiment. For *U. cakilefolia* and *D. pinnata* inflorescences in the same low density – high dispersion arrangement (i.e. LDD treatment), species identity significantly affected visitation

rate ($X^2 = 4.45$, $df = 1$, $P = 0.035$) with *U. cakilefolia* receiving significantly more visits than *D. pinnata* ($z = 2.18$, $P = 0.029$). However, visitation rates did not vary between Experiments 1 and 2 which differed in the level of dispersion ($X^2 = 0.47$, $df = 1$, $P = 0.494$).

Fruit set

Plant density and/or dispersion patterns had significant effects on fruit set for both *D. pinnata* (likelihood ratio tests, Exp. 1: $X^2 = 89.94$, $df = 3$, $P < 0.001$, Fig. 3.5a; Exp. 2: $X^2 = 35.53$, $df = 3$, $P < 0.001$; Fig. 3.5b) and *U. cakilefolia* (Exp. 1: $X^2 = 60.97$, $df = 3$, $P < 0.001$, Fig. 3.5c; Exp. 2: $X^2 = 171.86$, $df = 3$, $P < 0.001$, Fig. 3.5d).

Fruit set patterns did not reflect variation in visitation rates among treatments (Fig. 3.4 vs. Fig. 3.5; Table 3.1). In direct contrast to the visitation rate results, fruit set of inflorescences at high density (HD treatment) was significantly higher than at low density (LD treatment) in three of the four species-experiment combinations (*D. pinnata*, Exp. 1 and 2; *U. cakilefolia*, Exp. 2; Tukey's contrasts, $P < 0.05$), a pattern consistent with the presence of an intraspecific mate availability effect (Fig. 3.5). In three cases (*D. pinnata*, Exp.2; *U. cakilefolia*, Exp. 1 and 2) plants in the LDC treatment set more fruit than in the LDD treatment (Tukey's contrasts, $P < 0.05$). This pattern was also not evident in the visitation rate results (Fig. 3.4), consistent with the predictions for an effect of heterospecific interference on fruit set (Table 3.1).

When comparing fruit set of plants at low density and high probability of heterospecific interference (LDD treatment) in Experiment 1, proportion fruit set of *U. anthemoides* (0.61 ± 0.03) was similar to *U. cakilefolia* (0.61 ± 0.08 ; $z = -0.53$, $P = 0.995$) whereas fruit set of *D. pinnata* was significantly lower at 0.33 ± 0.08 ($z = 8.59$, $P < 0.001$). In Experiment 2, where the potential for an interference effect in the LDD treatment was increased, fruit set of *U. cakilefolia* (0.37 ± 0.08 ; $z = -8.31$, $P < 0.001$) and *D. pinnata* (0.05 ± 0.04 ; $z = -7.67$, $P < 0.001$) was significantly reduced compared to Experiment 1. In contrast, fruit set of *U. anthemoides* (0.74 ± 0.03) actually increased slightly ($z = 3.60$, $P = 0.004$), as was evident from a significant species \times experiment effect ($X^2 = 107.97$, $df = 2$, $P < 0.001$), suggesting that the ability to self-fertilise autonomously can ensure fecundity in low density/high dispersion scenarios.

Discussion

Pollinator visitation data suggest that intraspecific competition for pollinators had a negative effect on fecundity (Table 3.1). In contrast, visitation data provide no support for four of the other density/dispersion dependent mechanisms (intraspecific facilitation, interspecific facilitation, interspecific pollinator limitation and rarity disadvantage) which could potentially affect variation in fecundity. If we were to consider fruit set independently of the pollinator visitation rate data, fruit set patterns would suggest the influence of several density/dispersion related mechanisms (Table 3.1). But, since pollinator visitation rates and fruit set patterns need to be considered simultaneously to unravel the mechanisms involved, we can reject intraspecific facilitation, interspecific facilitation, interspecific pollinator limitation and rarity disadvantage as mechanisms affecting fecundity in our system.

Plants in low density patches (LD treatment) as well as plants at low relative abundance scattered among heterospecifics (LDD treatment) consistently performed poorly in terms of fruit set (Fig. 3.5). This reduction in fecundity was not the result of a significant reduction in pollinator visitation to inflorescences in these treatments. Instead, mechanisms affecting the transfer of conspecific vs. heterospecific pollen most likely resulted in the observed fruit set patterns. Fecundity was high when species were at high density (HD treatments), this despite negative density dependent effects on visitation rates through intraspecific competition for pollinators. The negative effects of intraspecific competition were outweighed by the positive effects of increased mate availability and/or decreased interference at high conspecific densities. Fecundity was also high when individuals were aggregated despite being at low density (LDC treatments), a pattern that can only be attributed to reduced heterospecific interference.

Thus at the community-level scale of our study (within a 100×100m area), localized changes in pollinator visitation rates associated with our experimental treatments did not strongly affect fecundity. However, we cannot rule out the possibility that differences in visitation rates at broader spatial scales (e.g. due to landscape-level changes in pollinator abundance) may have stronger effects on plant fecundity.

Effects of conspecific density on pollination and fecundity

Pollinator-mediated Allee effects in plant populations may arise when populations are too small, too isolated, or too sparse to receive sufficient pollinator visitation (e.g. Groom, 1998; Forsyth, 2003). However, recent studies also emphasise the importance of mate-finding in generating component Allee effects (reviewed in Gascoigne *et al.*, 2009). To tease apart the mechanisms behind Allee effects, it is necessary to examine both pollinator activity (e.g. pollen deposition or pollinator visitation rates) and fruit/seed set consequences of density or spatial aggregation. While we did not explicitly study Allee effects (positive associations between population size and fecundity), our results may have important implications concerning the mechanisms behind the Allee effect. Where other studies suggest that low fecundity in small populations is the result of lower pollinator visitation rates, we show that low fecundity in small or relatively low density populations may result from increased frequencies of IPT and decreased mate availability. Similar to our study, Moeller (2004) documented that seed set was more limited by pollen availability in small populations of *Clarkia xantiana* ssp. *xantiana* than in large populations. He suggested that low mate availability was the mechanism behind his observations, because pollinator visitation rates were not affected by population size. However, our results suggest that increased IPT with increasing heterospecific abundance can contribute toward a reduction in fecundity for individuals at low relative abundance.

Effects of dispersion on pollination and fecundity

Our results demonstrate that spatial aggregation of plants (clumping) enhances fecundity at low relative abundance. A potential explanation for high fruit set in the LDC treatment compared to the LDD treatment in our arrays (Fig. 3.5) is that monospecific patches may be more attractive to pollinators or are more likely to retain pollinators within the patch (Hanoteaux *et al.*, 2013). Under this scenario we would expect plants in the LDC treatment to receive more pollinator visits than plants in the LDD treatment; however, visitation rates did not differ between these treatments (Fig. 3.4). Based on this finding, and the fact that the dominant pollinators do not exhibit floral constancy (Ellis & Johnson, 2012), we attribute the observed reduction in fecundity of scattered individuals to the negative effects of heterospecific interference.

Intraspecific aggregation of individuals results in more intraspecific interactions than would be expected from the species' overall abundance and may play an important role in the

reduction of populations' vulnerability to pollinator-mediated Allee effects on fruit or seed production (Ghazoul, 2005; Hanoteaux *et al.*, 2013). Clumped spatial distribution patterns therefore reduce the frequency of interspecific interactions, and also reduce the frequency of IPT. IPT can affect female fitness by interfering with conspecific pollen adhesion and germination (Galen & Gregory, 1989) or by inhibiting ovule fertilisation and seed development (Thomson *et al.*, 1981), while with male fitness reduction occurs because pollen is lost to heterospecific flowers, reducing the amount of pollen transferred between conspecific flowers (pollen discounting; Lloyd, 1992). Several studies highlight the significant influence of dispersion patterns on pollinator-mediated interactions (e.g. Duncan *et al.*, 2004; Brys *et al.*, 2007). In one such study, plant aggregation was associated with increased fecundity in *Kniphofia linearifolia* (Duffy *et al.*, 2013). In their system the reduction in seed set resulted from reduced bird visitation rates in response to decreased conspecific aggregation, although no co-flowering heterospecifics were available to pollinators. In our study plant aggregation was also associated with increased fecundity; however, this was not the result of increased visitation rates but rather a decline in heterospecific interference.

Implications for the evolution of self-fertilisation

The evolution of autogamous selfing can alleviate the requirements for both pollinators and mates, thereby providing reproductive assurance under unpredictable or insufficient pollinator environments (Kalisz & Vogler, 2003; Kalisz *et al.*, 2004; Eckert *et al.*, 2006). In addition, self-fertilisation can mitigate the negative effects of low density on fecundity caused by low mate availability (Rodger *et al.*, 2013), pollinator competition (Rathcke, 1988) and hybridisation through IPT (Goodwillie & Ness, 2013).

The ability of autogamy to mitigate the negative effects of low density on fecundity in this system was observed by the inclusion of the autogamous species *U. anthemoides* in our experimental arrays. Fecundity of *U. anthemoides* was consistently high, and in contrast to the self-incompatible species, it was unaffected when individuals were at low density and scattered among heterospecifics. Since no pollinators were observed visiting this species, we attribute its consistently high fruit set (even in low density treatments) to its ability to reproduce autogamously. These findings suggest that the ability to autonomously self not only offers reproductive assurance under suboptimal pollination conditions, but also under

conditions where the probability of heterospecific interference is high. Our results raise the interesting possibility that autogamy may evolve as a reproductive assurance response to highly dispersive seeds, if high dispersal causes individuals to be scattered among a background of heterospecific individuals. De Waal *et al.* (2014) found some evidence in support of this when they documented an association between dispersal ability and breeding system in annual Asteraceae in Namaqualand. They identified two distinct syndromes: species that are highly dispersive and self-compatible (including *U. anthemoides*), and those that are less dispersive and self-incompatible (including *U. cakilefolia*). From another perspective, a selfing strategy may be optimal for such highly dispersive, scattered individuals, because traits associated with the ‘selfing syndrome’ (e.g. reduced flower size and showiness; Armbruster *et al.*, 2002) may cause pollinators to avoid them altogether and consequently minimise the probability of heterospecific interference.

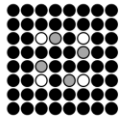
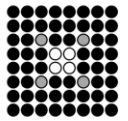
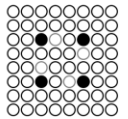
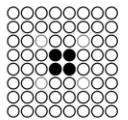
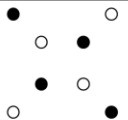
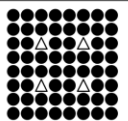
Conclusions

Spatial dispersion patterns of plants and conspecific density can have a major effect on the fecundity of individuals in multi-species co-flowering communities. Our study emphasises the importance of heterospecific interference and mate availability on fecundity. Both of these mechanisms are affected by plant density and dispersion, and operate independently of quantitative variation in visitation rates. We also highlight the importance of community structure: at low abundance and scattered dispersion patterns, individuals in our experimental arrays exhibited very low fruit set. Self-compatibility, however, ensured consistent fruit set and may provide a mechanism to enhance fecundity for species with scattered distributions in a community, such as species with highly dispersive propagules.

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| Experimental design | Treatment: Focal species (filled circles) = <i>D. pinnata</i> | Treatment: Focal species (open circles) = <i>U. cakilefolia</i> | Treatment: Focal species (open triangles) = <i>U. anthemoides</i> |
|--|---|---|---|
|  | High density (HD) | Low density, dispersed (LDD) | - |
|  | High density (HD) | Low density, clumped (LDC) | - |
|  | Low density, dispersed (LDD) | High density (HD) | - |
|  | Low density, clumped (LDC) | High density (HD) | - |
|  | Low density (LD) | Low density (LD) | - |
|  | NA | - | Low density, dispersed (LDD) |

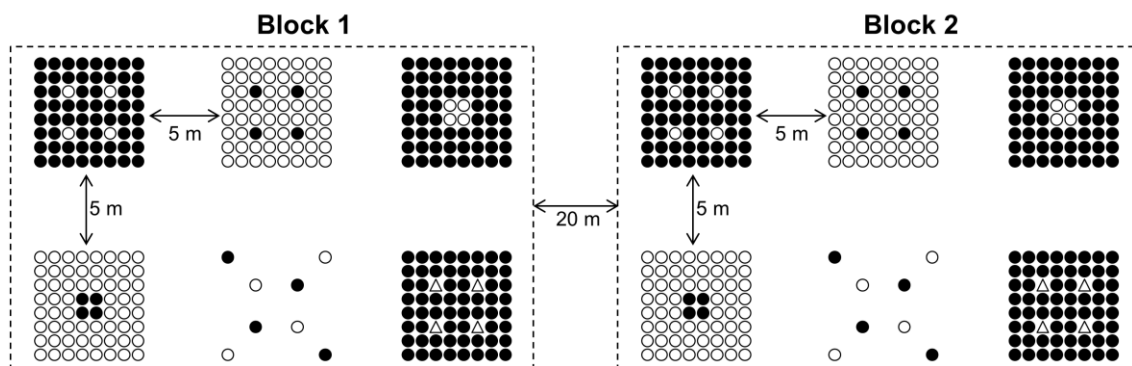


Fig. 3.1. Design and layout of experimental arrays with three annual Asteraceae species: the self-incompatible *Dimorphotheca pinnata* (filled circles) and *Ursinia cakilefolia* (open circles), and the autogamous *U. anthemoides* (triangles). Every experimental unit (array) represents a different arrangement of two species varying in relative abundance, dispersion and overall density. Each symbol represents a pot containing three plants. Pots with focal plants in the high density (HD) treatments are indicated in grey. To maintain consistent abundance of inflorescences in the low density treatments (LDD, LDC and LD), only one inflorescence per pot was allowed to flower. Fruit set of all focal inflorescences was determined for each treatment. Dashes indicate absence of the species in the array. NA

indicates that individuals of the species were not used in analyses. The six arrays formed one block, and blocks were replicated five times. The entire experiment was repeated twice (Experiments 1 and 2).



Fig. 3.2. Inflorescences of (a) *Ursinia cakilefolia* ($\times 1.7$), (b) *Dimorphotheca pinnata* ($\times 1.4$) and (c) *Ursinia anthemoides* ($\times 0.9$) used as study species in experimental arrays.

Experimental arrays (see Fig. 3.1) include: (d) *D. pinnata* in the high density (HD) treatment and *U. cakilefolia* in the low density, clumped (LDC) treatment; (e) *U. cakilefolia* in the HD treatment and *D. pinnata* in the low density, dispersed (LDD) treatment; (f) *U. cakilefolia* and *D. pinnata* in the low density (LD) treatment.

| Interaction | Mechanism | Density effect | Dispersion effect | Prediction for fruit set | Prediction for visitation rate |
|----------------------|---|----------------------|-------------------|--------------------------|--------------------------------|
| Intraspecific | | | | | |
| | <i>Facilitation</i> : positive density effect; more conspecific flowers attract more pollinators | + | NA | | Same |
| | <i>Mate availability</i> : more conspecific flowers in proximity enhance pollen transfer | + | NA | | No prediction |
| | <i>Competition for pollinators</i> : not enough pollinators to pollinate all flowers | - | NA | | Same |
| Interspecific | | | | | |
| | <i>Facilitation</i> : magnet species attracts pollinators to rare species; total density of patch attracts more pollinators | + | NA | | Same |
| | <i>Competition for pollinators</i> : not enough pollinators to pollinate all flowers (pollinator limitation) | - | NA | | Same |
| | <i>Competition for pollinators</i> : common species attracts more pollinators than rare species (rarity disadvantage) | - (relative density) | NA | | Same |
| | <i>Interference</i> : heterospecific pollen transfer or reduced conspecific pollen transfer efficiency reduces reproductive success | NA | - | | No prediction |

Fig. 3.3. Predicted inequalities between array treatments for pollinator visitation rates and fruit set derived from the various mechanisms by which intra- and interspecific interactions may affect the reproductive success of a self-incompatible focal species (filled circles), co-flowering with another species (open circles) in a community. Effects (positive or negative) of density (low or high) and dispersion (clumped or scattered) on fruit set and pollinator visitation rate are indicated for each mechanism. Expected inequalities for fruit set and visitation rates between experimental array treatments are shown in each case, where filled circles represent the focal species and where HD = high density treatment; LDD = low density, dispersed treatment; LDC = low density, clumped treatment; LD = low density treatment (Fig. 3.1). We have extracted the treatment comparisons which are least likely to be confounded by mechanisms other than the one under consideration, resulting in predictions for combined pollinator visitation and fruit set patterns unique to each underlying mechanism.

* Only one of the HD arrays are shown here, although fruit set and visitation rates of plants in the HD treatment were established from two different HD arrays where only the arrangement of the rare species differed (see Fig. 3.1).

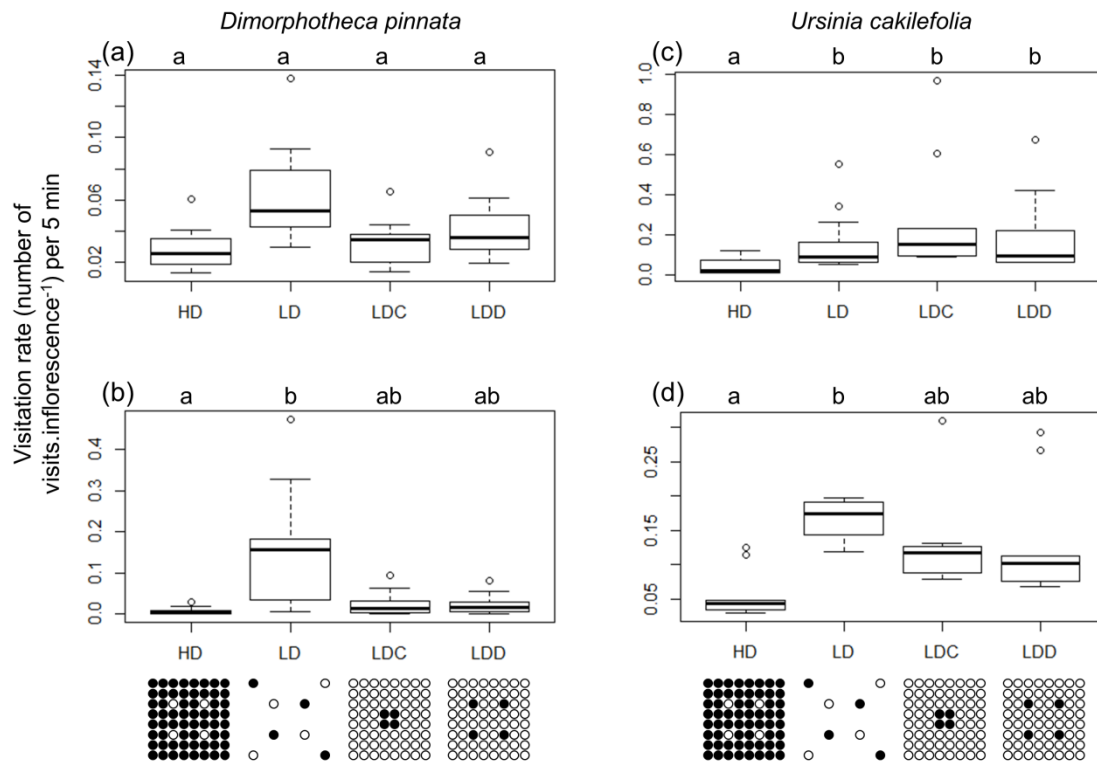


Fig. 3.4. Fitted estimates of pollinator visitation rates (number of visits.inflorescence⁻¹) per five-minute observation period in experimental arrays of *Dimorphotheca pinnata* in (a) Experiment 1 and (b) Experiment 2, and *Ursinia cakilefolia* in (c) Experiment 1 and (d) Experiment 2. Experimental arrays are indicated as in Fig. 3.1 where filled circles represent *D. pinnata* and open circles represent *U. cakilefolia*. Treatments are: HD = high density; LD = low density; LDC = low density, clumped; LDD = low density, dispersed. Only one of the HD arrays are shown here, although visitation rate of plants in the HD treatment was established from pooled data from two different HD arrays where only the arrangement of the rare species differed (see Fig. 3.1). Means that share the same letter are not significantly different ($P > 0.05$, Tukey's contrasts for multiple comparisons of means). Note that scale differs between graphs. Bold lines indicate the medians, boxes the interquartile range, whiskers the ranges and points are outliers.

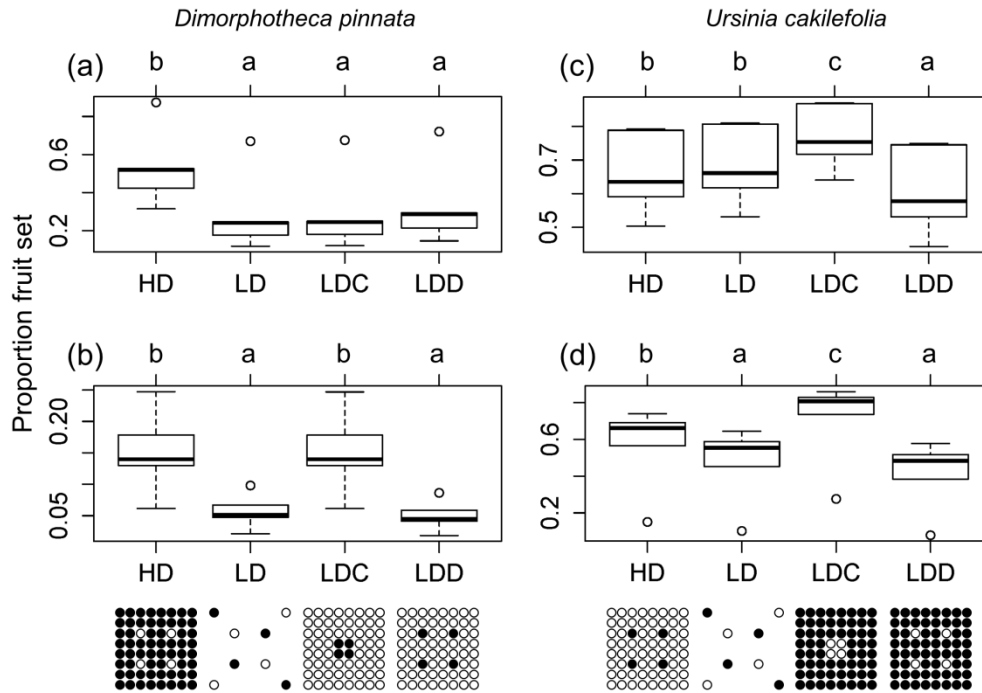


Fig. 3.5. Fitted estimates of proportion fruit set of *Dimorphotheca pinnata* in four experimental treatments in (a) Experiment 1 and (b) Experiment 2, and *Ursinia cakilefolia* in (c) Experiment 1 and (d) Experiment 2. Treatments are: HD = high density; LD = low density; LDC = low density, clumped; LDD = low density, dispersed. Experimental arrays are indicated as in Fig. 3.1 where filled circles represent *D. pinnata* and open circles represent *U. cakilefolia*. Only one of the HD arrays are shown here, although fruit set of plants in the HD treatment was established from pooled data from two different HD arrays where only the arrangement of the rare species differed (see Fig. 3.1). Means that share the same letter are not significantly different ($P < 0.05$; Tukey's contrasts for multiple comparisons of means). Note the different scale in B and C. Bold lines indicate the medians, boxes the interquartile range, whiskers the ranges and points are outliers.

Table 3.1. Summary of hypothesised mechanisms, predicted pollinator visitation rate and fruit set contrasts and visitation rate and fruit set results of experimental arrays with two self-incompatible annual Asteraceae species, *Dimorphotheca pinnata* and *Ursinia cakilefolia*, in two experimental runs (Experiments 1 and 2). Predicted visitation rate contrasts that differ from those for fruit set are indicated in square brackets. Bold type indicates likely mechanisms operating in each species-experiment combination, i.e. instances where combined visitation rate and fruit set data support the predicted contrasts.

| Hypothesis | Contrast [contrast for visitation rate, if different] | <i>D. pinnata</i> Exp. 1 | | <i>D. pinnata</i> Exp. 2 | | <i>U. cakilefolia</i> Exp. 1 | | <i>U. cakilefolia</i> Exp. 2 | |
|---|---|--------------------------|-----------|--------------------------|-----------|------------------------------|-----------|------------------------------|-----------|
| | | Visitation rate | Fruit set | Visitation rate | Fruit set | Visitation rate | Fruit set | Visitation rate | Fruit set |
| Intraspecific facilitation | HD > LD | No | Yes | No | Yes | No | No | No | Yes |
| Mate availability | HD > LD [No prediction] | - | Yes | - | Yes | - | No | - | Yes |
| Intraspecific competition for pollinators | LD > HD | No | No | Yes | No | Yes | No | Yes | No |
| Interspecific facilitation | LDD and LDC > LD | No | No | No | No | No | No | No | No |
| Interspecific competition for pollinators (pollinator limitation) | LD > LDD and LDC | No | No | No | No | No | No | No | No |
| Interspecific competition for pollinators (rarity disadvantage) | HD > LDD and LDC | No | Yes | No | No | No | No | No | No |
| Interference | LDC > LDD [No prediction] | - | No | - | Yes | - | Yes | - | Yes |

Chapter 4

**Geographic variation in seed heteromorphism of annual and perennial
Dimorphotheca (Asteraceae) in relation to climatic unpredictability**

Abstract

Bet-hedging strategies allow plants to respond to environmental variance. For example, seed dormancy and dispersal may spread risk through time and space in temporally and spatially heterogeneous environments, respectively. Life history traits (annual vs. perennial growth habit) are expected to affect the relative importance of different risk-reducing strategies. Selection on dispersal and dormancy related traits in populations is also expected to vary with proximity to the species' range edge, where suitable habitat may be sparse or unpredictable. Seed heteromorphic plants, which produce propagules that differ in dispersability and germination behaviour, are ideal to investigate investment in dispersal vs. dormancy in different environments. We sampled populations of three annual and two perennial *Dimorphotheca* (Asteraceae) species across the Succulent Karoo biome and the Cape Floristic Region, South Africa, for fruit and floret production. We compared the number of central, dispersive fruit (mainly non-dormant) and the proportion of peripheral, non-dispersive (mainly dormant) fruit between annuals and perennials. Using mean winter rainfall and the coefficient of variation (CV) of winter rainfall, we compared variation in the production of peripheral vs. central fruit in relation to climate unpredictability in *D. sinuata* and *D. pluvialis*. Perennial species produced very few peripheral propagules compared to annuals, supporting the prediction that longevity and dormancy are alternative temporal risk-reducing strategies. However, our results provide little support for theoretical predictions of bet-hedging strategies in unpredictable or range edge habitats. Although *D. pluvialis* populations in unpredictable environments produced more dispersive and dormant fruit, this pattern was weak when controlling for inflorescence size, suggesting that constraints on inflorescence development may limit the ability of selection to alter relative allocation to dispersal and dormancy in this system. Instead, observed fruit set patterns may reflect a strong influence of local environmental factors, obscuring the pattern across broad climatic gradients. Our results emphasise that life history significantly affects the relative investment in different dispersal strategies. In addition, the bet-hedging function of the seed heteromorphism may be a sufficient risk-reducing strategy for annuals in climatically unpredictable habitats, regardless of the proportions of fruit morphs.

Introduction

Temporal variation at various scales is characteristic of all natural environments. Organisms can respond to environmental variance through rapid adaptive evolution (adaptive tracking) or phenotypic plasticity. Alternatively they can evolve strategies to reduce risk through bet-hedging, where spatial or temporal variation in fitness is reduced (and geometric mean fitness is enhanced) at the expense of reduced arithmetic mean fitness (Slatkin, 1974; Seger & Brockmann, 1987; Philippi & Seger, 1989; Simons, 2011).

Bet-hedging strategies are particularly important in arid systems where the amount and distribution of rainfall events can be unpredictable (Gutterman, 1994). For example, many desert annuals spread the risk of reproductive failure in time through delayed germination. If all seeds germinate at once after a rainfall event, they could face local extinction if there is no follow-up rain, or if the rainfall event occurred when conditions are unsuitable for seedling growth, establishment or reproduction. Producing a fraction of dormant seed ensures that at least some offspring survive in the soil seed bank (Cohen, 1966; Venable, 2007; Gremer *et al.*, 2012; Gremer & Venable, 2014). Here one may expect an increase in the proportion of dormant seeds produced as the risk associated with germination (i.e. the probability of reproductive or growth failure) increases (Ellner, 1985a; Seger & Brockmann, 1987; Venable & Brown, 1988). In contrast to delayed germination, dispersal allows for risk to be spread in space. In spatially heterogeneous environments, where the habitat is divided into patches of different favourability, selection may favour dispersive propagules (Gadgil, 1971; McPeck & Holt, 1992) so that the detrimental effects of local extinction are buffered by the positive effects of reaching favourable patches (Levin *et al.*, 1984).

The relative importance of dormancy vs. dispersal may vary across species' geographic ranges. This may be especially true at the edges of a species' range where environmental conditions are expected to be more variable in space and time than they are at the centre of the range (Sexton *et al.*, 2009). Consequently stronger selection on life history traits that affect dispersal and dormancy is expected at the range margins than at the range centres (McPeck & Holt, 1992; Volis *et al.*, 2004; Phillips *et al.*, 2006; Hughes *et al.*, 2007; Dytham, 2009).

However, in a previous study of annual Asteraceae in South Africa, no effect of range position on dispersal ability was evident (De Waal *et al.*, 2014).

Other life history traits, specifically annual vs. perennial growth habit, may also affect selection on dispersal or dormancy. For example, perennial, iteroparous (reproducing more than once in a lifetime) plants face an increase in the probability of encountering favourable conditions for reproduction, by investing in longevity as survival strategy (Bulmer, 1985; Ehrlen & Van Groenendael, 1998; Zeineddine & Jansen, 2009). This negates the need for delayed germination to evolve in long-lived, iteroparous plants, so that dormant seed banks are predicted to be associated with annuals rather than perennials (Tuljapurkar, 1990; Rees, 1994). In addition, annuals and perennials may differ in their dispersal ability, because annuals often occur in habitats that are more unpredictable and variable, and dispersal increases their colonising ability (Olivieri *et al.*, 1983; see Venable & Levin, 1983 and references therein). Alternatively, increased dispersal ability may be selected in perennial plants to avoid kin competition (Cook, 1980). Indeed, in a comparative study of several thousands of species of Asteraceae, Venable & Levin (1983) found that morphological adaptations for dispersal in space were significantly more prevalent among perennial plants than annual plants.

Seed heteromorphism, the production of seeds that differ in form and/or behaviour by a single individual, is another well-documented bet-hedging strategy and is known from 18 angiosperm families (reviewed in Venable, 1985; Imbert, 2002). This strategy is particularly prevalent in the Asteraceae where differentiation between the single-seeded fruit (achenes) mainly occurs among the periphery and centre of the capitulum (hereafter referred to as peripheral and central fruit). Often, fruit morphs differ in their dispersal ability and dormancy capacity, so that propagules from a single individual are spread both in space and in time. In the Asteraceae, the number of peripheral florets is determined by the number of phyllotactic spirals in the capitulum, a highly canalised trait (Battjes *et al.*, 1993; Harris, 1995), and shows little plasticity. In contrast, the number of central florets is regarded as a highly plastic trait determined by the size of the capitulum and is positively correlated with the fecundity of the head (Imbert *et al.*, 1999; Imbert & Ronce, 2001). Consequently, developmental constraints may largely influence morph proportions. However, fruit and seed production in plants is also

affected by phenotypic plastic responses, pollen limitation or resource allocation (e.g. Campbell & Halama, 1993; Imbert & Ronce, 2001). Seed heteromorphic plants are therefore ideal systems to investigate variation in dispersal vs. dormancy in relation to environmental factors and life-history traits.

Dimorphotheca (Asteraceae) is a southern African genus of predominantly seed heteromorphic plants, comprising both annual and perennial species. We focused on spring-flowering (July – October) species in the winter rainfall regions of South Africa and southwestern Namibia, namely the arid Succulent Karoo biome, and the more mesic Cape Floristic Region (the Greater Cape Floristic Region; Born *et al.*, 2007). In these regions, winter rainfall (April – September) is regarded as the most ecologically significant variable for germination and flowering (Cowling *et al.*, 1999).

In *Dimorphotheca*, winged achenes originate from the disk florets and typically germinate quickly and easily, resulting in robust and highly competitive individuals. On the other hand, peripheral achenes, originating from the ray florets, do not possess dispersal structures and dormancy seems to be induced by the physical and chemical qualities of the relatively thick pericarp (Correns, 1906; Becker, 1913; Beneke, Van Rooyen, *et al.*, 1992; Beneke, Von Teichman, *et al.*, 1992; Beneke *et al.*, 1993). Consequently, dispersal in space and time by the offspring of the same individual may reduce the risk associated with spatial and temporal heterogeneity.

Previous studies on seed heteromorphism in *Dimorphotheca* focused only on plants from a single locality and only investigated morph characteristics of two annual species. In this study we conducted an investigation of seed heteromorphism in annual and perennial *Dimorphotheca* species across a broad geographic range in southern Africa. We ask: 1) Do annual and perennial *Dimorphotheca* species differ in their production of dispersive, non-dormant (central) vs. non-dispersive, dormant (peripheral) fruit?; 2) Is there significant geographic variation among populations of *D. sinuata* and *D. pluvialis* in the production of ray vs. disk florets and peripheral vs. central fruit?; 3) Can climatic variables, particularly the unpredictability of winter rainfall, predict variation in floret and/or fruit traits of *D. sinuata* and *D. pluvialis*?; 4) Do populations of

D. sinuata and *D. pluvialis* on the range edge vs. range centre differ in the relative production of the two fruit morphs, i.e. does investment in dispersal and dormancy vary across distribution ranges?

Materials and Methods

Study species

Our study focused on three annual and two perennial *Dimorphotheca* (Asteraceae) species (Fig. 4.1). The annual species included the dimorphic *D. sinuata* DC. and *D. pluvialis* (L.) Moench and the trimorphic *D. polyptera* DC. *Dimorphotheca sinuata* (Fig. 4.1a-c) naturally occurs across the arid Namaqualand region (Fig. 4.2), and is often one of the dominant species in the region's spectacular annual spring flowering displays. *Dimorphotheca pluvialis* (Fig. 4.1f) occurs on sandy flats and slopes in Namaqualand and the Western Cape, where it is particularly prominent on the coastal plain (Fig. 4.2). In both of these species disk florets give rise to winged, dispersive achenes with high germination probability, whereas ray florets result in unwinged fruit with low dispersal ability but high dormancy (Chapter 5). However, the third annual, *Dimorphotheca polyptera*, produces three fruit morphs: disk florets give rise to winged achenes similar to the other annual species, but ray florets result in two types of achenes, one resembling the unwinged peripheral achenes of *D. sinuata* and *D. pluvialis* and the other resembling a three-winged variant of the latter (Fig. 4.1d). However, both types of peripheral achenes are highly dormant (Chapter 5). *Dimorphotheca polyptera* (Fig. 4.1d, e) occurs in more arid parts of Namaqualand and the Richtersveld, and extends further into the Northern Cape and Namibia.

The perennial shrub *Dimorphotheca tragus* (Aiton) B.Nord. (Fig. 4.1i, j) occurs in rocky hills and mountain slopes across Namaqualand and the Richtersveld. Its central florets give rise to large, non-dormant winged achenes resembling those of the annual species (Chapter 5). Fully developed peripheral achenes are extremely rare (present study) and lack any dispersal structures. Their germination behaviour is unknown. The other perennial shrub in this study, *Dimorphotheca cuneata* (Thunb.) Less. (Fig. 4.1g, h) occurs predominantly in the eastern

Succulent Karoo and Nama Karoo biomes of western and central South Africa. Its central fruits resemble those of *D. tragus* (Fig. 4.1g), but peripheral achenes are occasionally found (present study). In contrast to the dormant peripheral achenes of annual *Dimorphotheca* species, peripheral achenes of *D. cuneata* are not dormant (Chapter 5). To the best of our knowledge no other studies have investigated seed heteromorphism in perennial *Dimorphotheca*.

Sampling

We sampled densely across the southern and western parts of the winter rainfall region in the Western and Northern Cape provinces of South Africa. We also sampled in the southwestern region of Namibia as well as eastward into the summer rainfall region along the Orange River and into the Karoo. These regions largely cover the distribution ranges of *D. sinuata* and *D. pluvialis*, and the western (winter-rainfall) parts of *D. polyptera* and *D. cuneata*'s distribution ranges. We also sampled *D. tragus*, which also occurs within these regions, although populations with fruit were scarce and plants were often heavily damaged by herbivores. Sampling took place during August – September 2007 and 2011 - 2013.

To determine the number of disk and ray florets in populations of *D. sinuata* and *D. pluvialis*, we sampled 15 and 14 populations, respectively. One inflorescence from 4 – 40 individuals per population (mean = 18.2 ± 7.48 SD and 18 ± 6.50 for *D. sinuata* and *D. pluvialis*, respectively) was dissected and the number of female-fertile disk florets and ray florets were counted. The number of central and peripheral achenes was determined in 58 populations of *D. sinuata* and 32 of *D. pluvialis* (Figs. S4.1 and S4.2; Table S4.1). In addition, the number of involucre bracts of inflorescences (an indication of the size of the inflorescence) was counted in a subset of these populations (32 and 17 *D. sinuata* and *D. pluvialis* populations, respectively). Since mature fruits tend to fall off the infructescence fairly quickly after maturation and drying, we collected 1 – 3 fully developed but immature (still moist and green) infructescences from 3 – 28 individuals per population (mean per population = 17.12 ± 5.03 SD and 19.34 ± 4.37 for *D. sinuata* and *D. pluvialis*, respectively). We also sampled four populations of *D. polyptera*, five populations of *D. tragus* and four populations of *D. cuneata*. In *D. polyptera*, both winged and wingless peripheral fruit were counted as 'peripheral fruit'. Where more than one infructescence

was sampled per individual, we used the average number of central or peripheral fruit and involucre bracts in analyses. In all species only achenes with firm embryos were counted as fruit. The GPS coordinates and number of individuals sampled for each population is reported in Table S4.1. Populations that were obviously the result of garden escapes or roadside dispersed populations were avoided, i.e. we only sampled naturally occurring populations.

Measures of climatic unpredictability

Rainfall data were obtained from the South African Weather Bureau for 48 weather stations in the Northern Cape and Western Cape provinces, with an average of 35.90 ± 2.53 SE years' daily rainfall records per station (range 3 – 63 years). Since our study species are predominantly restricted to the winter-rainfall region of South Africa and flower in late winter – spring, we only used rainfall records between the months of April – September (hereafter called winter rainfall), because these are likely biologically most significant (Cowling *et al.*, 1999). Monthly totals were calculated and months with missing data were excluded. The following climatic variables were calculated for each weather station: a) Coefficient of variation (CV) of winter precipitation across years, calculated as the standard deviation (SD) of the average winter rainfall per year divided by the mean (this variable represents the annual predictability of winter rainfall at the station); b) Mean winter precipitation, calculated as the average of the total winter rainfall per year; c) CV of precipitation across winter months, calculated as the CV of monthly rainfall from April – September, averaged across years (this variable indicates the variability of rainfall events between months during the winter); d) Mean precipitation and CV for rainfall separately for the months of April – June and July – September.

We tested for correlations between these climatic variables using the *corrplot* package (Wei, 2013) in R (R Core Team, 2013). The seven climatic variables were significantly correlated (Fig. S4.3) and therefore we used only two variables, namely mean winter precipitation and interannual CV of winter precipitation, in subsequent analyses with fruit and floret traits. The CV of winter precipitation was included because it represents a biologically meaningful measure of rainfall predictability across years, and clear predictions exist for

variation in dispersal and dormancy in relation to temporal unpredictability (e.g. Cohen, 1966; Snyder, 2006; Siewert & Tielbörger, 2010).

Mean winter precipitation and CV of winter precipitation from the closest weather station were used in analyses of fruit and floret traits in our study populations. In cases where two weather stations were equidistant, the average of the two stations' values was used. The average distance from each study population to the closest weather station was $12.14 \text{ km} \pm 1.07 \text{ SE}$ (range 0.4 – 40.1 km).

Range edge proximity

To establish fine-scale distribution ranges for *D. sinuata* and *D. pluvialis*, we recorded their presence during our sampling effort and also obtained presence data for both species from the South African National Biodiversity Institute (accessed through the SIBIS portal, sibis.sanbi.org, 2014-08-08). SIBIS offers access to occurrence records obtained from numerous data sources and herbarium collections. Occurrence record localities are given in quarter degree grid squares. The SIBIS data set was cleaned by checking all outlying data points (points disconnected from the main distribution) and removing them if they were 1) listed as ex hort (garden escapes), 2) obvious misidentifications (e.g. description of orange flower colour for *D. pluvialis*), or 3) if the record was collected before 1970 with no description of the locality or specimen and therefore no way to verify the specimen. Record points and quarter degree grid squares were connected to form the smallest polygon. Field data were collected over four years and across the distribution ranges of these species. We also sampled beyond the known ranges of each species, and we are confident that we have accurate depictions of their current distribution ranges.

To explore variation in investment in dormancy and dispersal in relation to geographic position, we used different measures of range edge proximity for populations of *D. sinuata* and *D. pluvialis*. Firstly, we measured the shortest distance to the range edge, regardless of direction. Secondly, because the northern and eastern range edges are most likely climatically controlled borders, where winter rainfall transitions into summer rainfall, we also measured the distance from each population to the range edge along straight lines to the north and east. In addition to

distances to the range edges, we explored variation in populations' fruit production in relation to latitude and longitude. Because we cannot assume a real gradient in habitat suitability from the core to the edge of the range, we also categorised populations as 'range edge' if they occurred within 0-4 km from the established northern or eastern range edge only, whereas populations were categorised as 'central' if they occurred more than 20 km from any edge for *D. sinuata*, or more than 10 km for *D. pluvialis*. These distances were chosen as cut-offs because they approximately represent the 25th and 75th percentiles, respectively. Populations that occurred between 4-20 km or 4-10 km from any range edge (for *D. sinuata* and *D. pluvialis*, respectively) were not included in this analysis. Fifteen central and 14 range-edge populations were sampled for *D. sinuata*, whereas ten and nine *D. pluvialis* populations were sampled in central and range-edge categories, respectively. Maps were created and measurements conducted in QGIS version 2.4.0.

Statistical analyses

All analyses were performed in R version 3.0.2 (R Core Team, 2013). To compare the number of central fruit (investment in dispersive propagules) and proportion of peripheral fruit (relative investment in dormant, non-dispersive propagules) produced by perennial vs. annual *Dimorphotheca* species, we used generalised linear mixed effects models (GLMM) with a poisson distribution and log link function (for number of central fruit) or a binomial distribution and logit link function (for proportion of peripheral fruit) with glmer in the lme4 package (Bates *et al.*, 2013). Life history (annual or perennial) was included as a fixed categorical factor. Species nested in life history and site nested in species nested in life history were included as random factors.

To analyse the variation in the number of central and peripheral fruit and disk and ray florets among populations of *D. sinuata* and *D. pluvialis*, population was used as predictor variable in simple ANOVAs for each species, using the function aov. To compare the population variability in the production of peripheral vs. central fruit, we compared the coefficient of variation (CV) of the number of peripheral and central fruits produced within each population using a paired t-test for each species. To compare the proportion of ray florets that set fruit with

the proportion of disk florets that set fruit in *D. sinuata* and *D. pluvialis*, we used non-parametric, paired Wilcoxon signed rank tests with the function `wilcox.test`. In addition, we tested for a correlation between mean numbers of ray and disk florets, and central and peripheral fruit in populations of *D. sinuata* and *D. pluvialis* using `cor.test`.

To investigate the relationships of the mean winter precipitation and CV of winter precipitation (calculated as standard deviation / mean across populations) with the latitude and longitude of *D. sinuata* and *D. pluvialis* populations, we performed multiple regressions with mean winter precipitation or CV of winter precipitation as dependent variables, and latitude, longitude and the latitude \times longitude interaction as predictor variables using the function `lm`. Significance of effects was obtained with the function `anova`. In *D. pluvialis*, two sites (Rondebosch and Site24.2) had exceptionally high winter rainfall means; consequently analyses with mean winter precipitation were performed with and without these outliers.

To test whether mean winter precipitation or the CV of winter precipitation can predict the mean number of central fruit, mean number of peripheral (non-dispersive, dormant) fruit and proportion peripheral fruit in *D. sinuata* and *D. pluvialis*, we conducted linear regressions using the function `lm`. With the number of central fruit as the dependent variable, we also included the mean number of involucre bracts as covariate, to control for variation in central fruit that can be attributed to inflorescence size. Linear regressions were also performed to investigate variation in the mean number of disk and ray florets and the mean number of involucre bracts with rainfall variables.

Because the relationship between ray and disk florets likely represents an allometric developmental response (larger inflorescences produce more florets), we investigated relationships between the values of residuals of regressions of population means of ray and disk floret numbers in *D. sinuata* and *D. pluvialis* (across 15 and 13 populations, respectively) with climatic variables, i.e. testing whether there is an association between departures from developmental constraints (allometric relationships) and environmental variables. The *D. pluvialis* population Rondebosch was omitted from these analyses with mean winter precipitation, on the grounds of being an extreme outlier. No relationships, linear or polynomial,

were evident between residuals of the ray-disk floret regression in *D. sinuata* and both climatic variables (results not shown), or between the *D. pluvialis* residuals and CV of winter precipitation. However, in *D. pluvialis* residuals vs. mean winter precipitation were analysed with a quadratic model. We also obtained the linear function of the regression of ray vs. disk florets across all individuals in *D. sinuata* and *D. pluvialis* to predict the maximum number of central fruit that can be produced given the number of ray florets (or involucre bracts). We used the difference between the maximum number of central fruit (i.e. disk floret number) and the observed number of central fruit as a measure of the number of central fruit not realised. This number was also expressed as a proportion of the maximum number of central fruit. Both the number and proportion of central fruit not realised were used as dependent variable in linear regressions with mean winter precipitation and CV of winter precipitation.

To examine the association between range edge proximity and the mean number of central fruit and proportion peripheral fruit per population, distance to closest range edge, distance to northern edge, distance to eastern edge, latitude and longitude were used as predictor variables in simple linear regression models with the function `lm`. Proportion peripheral fruit in *D. sinuata* was log-transformed to meet the assumptions of linear regressions. With the number of central fruit as dependent variable, the mean number of involucre bracts was also included as covariate to account for variation in inflorescence size. To compare the number of central fruit and the proportion of peripheral fruit among range edge and central populations for each species, we used non-parametric Wilcoxon rank sum tests (with the `wilcox.test` function).

Results

Seed heteromorphism in annual vs. perennial Dimorphotheca

Seed heteromorphism was evident in all five study species of *Dimorphotheca* that occur in Namaqualand. The perennial species included in this study (*D. tragus* and *D. polyptera*; Fig. 4.1 g-j) produced significantly more central (dispersive) fruit compared to annuals (GLMM, $z = 2.26$, $P = 0.024$), whereas the annual species (*D. sinuata*, *D. pluvialis* and *D. polyptera*; Fig. 4.1

a-f) produced a significantly higher proportion of peripheral, non-dispersive fruit ($z = -3.83$, $P < 0.001$; Fig. 4.2a, c, d). Only 0.2 % of the sampled *D. tragus* individuals produced peripheral fruit, and then no more than three per infructescence, although the number of involucre bracts per inflorescence (and therefore the number of potential peripheral fruit) ranged from 16 – 24 (mean = 20.40 ± 0.18 SE). Although *D. cuneata* produced fewer central fruit than *D. tragus* (Fig. 4.2a), the proportion peripheral fruit produced in *D. cuneata* was still only 10.4% of the total fruit set.

Geographic variation in seed heteromorphism in D. sinuata and D. pluvialis

Our study populations of *D. sinuata* and *D. pluvialis* occurred predominantly in the Succulent Karoo and Fynbos biomes of South Africa (Fig. S4.4) and geographic variation in seed heteromorphism was evident among populations. The number of central fruit ($F = 11.99$, $df = 57$, $P < 0.001$ and $F = 9.86$, $df = 31$, $P < 0.001$, respectively) and peripheral fruit ($F = 8.11$, $df = 57$, $P < 0.001$ and $F = 8.51$, $df = 31$, $P < 0.001$, respectively) differed significantly among populations of *D. sinuata* and *D. pluvialis* (Fig. S4.5; Table S4.1). Similarly, the mean number of disk florets ($F = 6.64$, $df = 15$, $P < 0.001$ and $F = 12.75$, $df = 14$, $P < 0.001$, respectively) and ray florets ($F = 4.19$, $df = 15$, $P < 0.001$ and $F = 8.44$, $df = 14$, $P < 0.001$, respectively) varied significantly between populations of *D. sinuata* and *D. pluvialis* (Fig. S4.5; Table S4.1). The mean number of ray and disk florets was significantly positively correlated in populations of *D. sinuata* ($r = 0.64$, $P = 0.012$; Fig. 4.3a) and *D. pluvialis* ($r = 0.84$, $P < 0.001$; Fig. 4.3b). Similarly, the production of central and peripheral fruit was significantly positively correlated in both species (*D. sinuata*: $r = 0.75$, $P < 0.001$, Fig. 4.3c; *D. pluvialis*: $r = 0.57$, $P = 0.001$, Fig. 4.3d).

In both species the proportion of ray florets that set fruit was significantly larger than the proportion of disk florets that set fruit ($V = 105$, $P < 0.001$ and $V = 66$, $P = 0.004$ for *D. sinuata* and *D. pluvialis*, respectively). Within populations, there was consistently more variation in the number of central fruit produced compared to the number of peripheral fruit. In *D. sinuata* the mean CV of the number of peripheral fruits produced (0.27 ± 0.02) was significantly smaller than the mean CV of the number of central fruit (0.56 ± 0.03 ; $t = -11.50$, $df = 57$, $P < 0.001$).

Similarly, in *D. pluvialis* variation in the number of peripheral fruits produced (mean CV = 0.24 ± 0.01) was significantly less than the number of central fruit produced (mean CV = 0.77 ± 0.11; $t = -5.20$, $df = 31$, $P < 0.001$).

Associations between fruit production and rainfall predictability

Mean winter precipitation and CV of winter precipitation varied significantly with the geographic position (latitude, longitude and latitude × longitude) of populations of *D. sinuata* and *D. pluvialis* (mean precipitation: $R^2 = 0.35$, $F_{3,54} = 9.76$, $P < 0.001$ and $R^2 = 0.58$, $F_{3,26} = 11.77$, $P < 0.001$, respectively; CV: $R^2 = 0.40$, $F_{3,54} = 12.02$, $P < 0.001$ and $R^2 = 0.46$, $F_{3,28} = 7.85$, $P < 0.001$, respectively). Mean winter precipitation at sites increased significantly toward the east ($F = 15.81$, $P < 0.001$ and $F = 18.21$, $P < 0.001$, respectively) and toward the south ($F = 9.72$, $P = 0.003$ and $F = 16.82$, $P < 0.001$, respectively) in *D. sinuata* and *D. pluvialis*. The effect of the latitude × longitude interaction on mean winter precipitation was marginally non-significant in *D. sinuata* ($F = 3.75$, $P = 0.058$) and not significant in *D. pluvialis* ($F = 0.27$, $P = 0.609$). CV of winter precipitation decreased toward the east in *D. sinuata* ($F = 26.37$, $P < 0.001$) but not *D. pluvialis* ($F = 2.00$, $P = 0.168$). In both species, CV decreased toward the south ($F = 5.67$, $P = 0.021$ and $F = 15.13$, $P = 0.001$ for *D. sinuata* and *D. pluvialis*, respectively). However, the effect of the latitude × longitude interaction on CV was significant in both species ($F = 4.04$, $P = 0.049$ and $F = 6.43$, $P = 0.017$ in *D. sinuata* and *D. pluvialis*, respectively).

Mean winter precipitation did not significantly predict the mean number of central fruit ($R^2 = 0.003$, $F_{1,56} = 0.14$, $P = 0.706$) or the mean proportion of peripheral fruit ($R^2 = 0.02$, $F_{1,56} = 1.17$, $P = 0.284$) across populations of *D. sinuata*. The mean number of involucre bracts was significantly associated with mean winter precipitation ($R^2 = 0.17$, $F_{1,30} = 6.03$, $P = 0.020$), but the pattern was driven by a single outlier (Kamberg), without which the relationship was not significant ($R^2 = 0.03$, $F_{1,29} = 0.77$, $P = 0.386$). Similarly in *D. sinuata*, there was no association between CV of winter precipitation and the mean number of central fruit ($R^2 = 0.001$, $F_{1,56} = 0.06$, $P = 0.800$), mean proportion peripheral fruit ($R^2 = 0.004$, $F_{1,56} = 0.20$, $P = 0.655$) or mean number of involucre bracts ($R^2 = 0.01$, $F_{1,30} = 0.39$, $P = 0.538$). Analyses with mean number of

central fruit were also not significant when accounting for inflorescence size (mean winter precipitation: $F = 0.43$, $P = 0.525$; CV of winter precipitation: $F = 1.52$, $P = 0.227$).

Although a significant negative relationship was evident between mean winter precipitation and the number of central fruit across all populations of *D. pluvialis* ($R^2 = 0.23$, $F_{1,30} = 9.13$, $P = 0.005$), this pattern was driven by two outliers from the Cape Peninsula (Rondebosch and Site 24.2) where mean annual winter rainfall was approximately 600 mm higher than the wettest sites among all the other populations. Excluding these two sites from the data set rendered non-significant results ($R^2 = 0.08$, $F_{1,28} = 2.45$, $P = 0.129$). Similarly, across all populations there was a significant positive relationship between mean winter precipitation and the proportion of peripheral fruit across all populations ($R^2 = 0.21$, $F_{1,30} = 7.86$, $P = 0.009$), but without the outliers Rondebosch and Site 24.2, this pattern was not significant ($R^2 = 0.04$, $F_{1,28} = 1.11$, $P = 0.302$). Across all populations, no relationship was evident between the mean number of involucre bracts and mean winter precipitation ($R^2 = 0.11$, $F_{1,15} = 1.84$, $P = 0.195$), but without the Rondebosch outlier this relationship was significantly negative ($R^2 = 0.26$, $F_{1,14} = 4.83$, $P = 0.045$). In *D. pluvialis* there was a significant positive association between CV of winter precipitation and mean number of central fruit (Fig. 4.5a; $R^2 = 0.17$, $F_{1,30} = 6.02$, $P = 0.020$) and mean number of peripheral fruit (Fig. 4.5b; $R^2 = 0.38$, $F_{1,30} = 18.07$, $P < 0.001$), and a marginally non-significant negative association between CV of winter precipitation and the proportion of peripheral fruit (Fig. 4.5c; $R^2 = 0.12$, $F_{1,30} = 3.98$, $P = 0.055$). However, the number of involucre bracts was not associated with CV of winter precipitation ($R^2 = 0.09$, $F_{1,15} = 1.45$, $P = 0.247$). When the number of involucre bracts was included as covariate in the model, mean winter precipitation did not significantly predict the number of central fruit ($F = 0.43$, $P = 0.525$). However, the positive relationship between the mean number of central fruit and CV of winter precipitation was still marginally significant ($F = 3.37$, $P = 0.091$). Residuals of the ray-disk floret regression (i.e. testing for more or less disk florets than predicted given the number of ray florets) was not associated with mean winter precipitation (quadratic model; Fig. 4.5a; $R^2 = 0.35$, $F_{2,10} = 2.63$, $P = 0.121$) or CV of winter precipitation (Fig. 4.5b).

Apart from a weak trend of more ray florets at sites with lower mean winter precipitation in populations of *D. pluvialis* ($R^2 = 0.25$, $F_{1,11} = 3.64$, $P = 0.083$), no relationships between

population means of ray and disk floret numbers and rainfall variables were evident (Table S4.2). No relationships were apparent between the number of central fruit not realised (i.e. the difference between the maximum and the observed number of central fruit) or the proportion of central fruit not realised and mean winter precipitation or CV of winter precipitation in either species (Table S4.3).

Associations between fruit production and range margin proximity

None of the measures of range edge proximity, including latitude and longitude, predicted the number of central fruit or the proportion peripheral fruit in populations of *D. sinuata* or *D. pluvialis* (Table S4.4). Mean numbers of central fruit did not differ between range edge and range centre populations in *D. pluvialis* (Wilcoxon rank sum test; $W = 29$, $P = 0.211$). Range centre vs. range edge populations also did not differ in mean numbers of central fruit in *D. sinuata* ($W = 105$, $P = 0.999$). The proportion peripheral fruit did not differ among central and range-edge populations in either *D. sinuata* ($W = 106$, $P = 0.983$) or *D. pluvialis* ($W = 57$, $P = 0.356$).

Discussion

*Dispersal and dormancy differences between annual and perennial *Dimorphotheca**

This study provides a novel investigation of seed heteromorphism across a large geographic region in the annual *D. sinuata*, *D. pluvialis* and *D. polyptera* as well as the first description of seed heteromorphism in two Namaqualand perennials, *D. tragus* and *D. cuneata*. Our results show significantly higher investment in dispersive propagules in perennial *Dimorphotheca* compared to annual species (Fig. 4.2). Moreover, the wind dispersal ability (determined from fall time) of these fruits are also higher than for annuals (Chapter 5). These results suggest selection for higher dispersability in perennial *Dimorphotheca*. However, although we sampled all *Dimorphotheca* species occurring in our study area, the number of species sampled for the two life history classes was low, thereby limiting the conclusions that may be drawn about

differences between annuals and perennials. Another major caveat is that we could not account for phylogenetic relatedness among species, because no phylogeny for this genus exists. Without knowledge of the independence of species, we cannot make inferences about the evolution of traits related to dispersal and dormancy in the genus.

Nevertheless, our findings support a previous comparative study that demonstrated a higher percentage of perennial species with plumed (dispersive) propagules compared to annual species across a worldwide sample Asteraceae (Venable & Levin, 1983). Dispersal may be favoured in perennials because adult plants may occupy suitable patches around the mother plant so that sites for recruitment are scarce. Moreover, perennials are often associated with low seed dormancy (e.g. Rees, 1993; see also Chapter 5), which may increase selection for dispersal as alternative risk-reducing strategy. In addition, the offspring of a perennial parent will benefit by escaping the parent's vicinity, because the chance of competition between the offspring and the larger adult plant is reduced (Cook, 1980; Venable & Levin, 1983). In a modelling study, Ronce *et al.* (2000) demonstrated that the evolutionary stable dispersal rate increases when the survival rate of iteroparous adults increases in response to kin selection. In annuals, on the other hand, there is no selection through parent-offspring competition on dispersal.

Perennial species also produced very low numbers of peripheral, non-dispersive fruit (Fig. 4.2) compared to annuals, given the number of ray florets available to produce potential fruit. This indicates that perennial species are not investing in the production of dormant propagules. Moreover, some evidence suggests that, at least in *D. cuneata*, the few peripheral fruit that are produced are not dormant at all (Chapter 5). Regardless of the mechanisms behind these patterns, our findings are in line with theoretical predictions that iteroparity should be associated with non-dormant seeds (Tuljapurkar, 1990; Rees, 1994), because longevity and dormancy both function as alternative temporal risk-reducing strategies (Bulmer, 1985). A limited number of comparative studies have found an association between low seed dormancy and adult longevity (Rees, 1993, 1996; Thompson *et al.*, 1998). In contrast to perennials species, in our three annual study species a high proportion of the available ray florets set fruit (Fig. S4.5) and these peripheral fruits were highly dormant (see Chapter 5). In addition, in *D. sinuata* and *D. pluvialis*, production of peripheral, dormant fruit as a proportion of the available ray florets was

significantly higher and less variable than for central fruit. In annuals, producing a fraction of dormant offspring may offset the possibility of population extinction if complete germination is followed by mortality under severely unfavourable environmental conditions (Cohen, 1966).

Geographic patterns of variation in seed heteromorphism of D. sinuata and D. pluvialis

Although we found substantial population-level variation in the numbers of dispersive and dormant propagules for *D. sinuata* and *D. pluvialis*, our data suggest that this variation is not structured along gradients of rainfall unpredictability or range edge proximity (also see De Waal *et al.*, 2014). In addition, we did not detect differences in fruit production among range edge and central populations, i.e. not assuming a continuous gradient in habitat suitability from the core to the edge. We did detect a pattern of more dispersive and more dormant fruit with increasing rainfall unpredictability in *D. pluvialis* populations (Fig. 4.4). However, there was a strong allometric relationship between ray and disk florets, which translated to significant correlations between the number of peripheral and central fruit (Fig. 4.3). When controlling for this allometric relationship by including the number of peripheral florets as covariate (a surrogate for inflorescence size), the relationship between the number of central fruit and rainfall unpredictability in *D. pluvialis* was weak. In addition, inflorescence size (the number of florets or involucre bracts) was not predicted by rainfall unpredictability, although there was a tendency for larger inflorescences at low rainfall sites. Adaptive responses to geographic variation in climatic unpredictability should be most strongly observed in correlations among floret numbers, since these traits are more likely to be developmentally controlled than fruit set. These findings suggest that selection imposed by rainfall unpredictability is constrained by allometry. We emphasise that we have sampled a large number of populations of *D. sinuata* and *D. pluvialis*, thereby increasing the power to detect clines within these species related to environmental unpredictability or range margin proximity if they existed, even if the trait in question is plastic and not only genetically determined.

Our results contradict expectations from the literature. While theory predicts that investment in dormancy, i.e. a higher proportion of dormant propagules, should increase in climatically less predictable parts of the range, or at the range edge (Ellner, 1985b; Seger &

Brockmann, 1987; Venable & Brown, 1988; see also Table 1.1 in Chapter 1), we find no evidence for an influence of rainfall unpredictability on allocation to dormancy in *Dimorphotheca*. Instead, we find some evidence, albeit weak, for higher investment in dispersive fruit in *D. pluvialis* in climatically unpredictable areas. This is somewhat surprising as dispersal is generally expected to not be a particularly effective strategy under temporal climatic unpredictability (Ellner & Shmida, 1981; Venable & Brown, 1988; Snyder, 2006; Venable *et al.*, 2008; Siewert & Tielbörger, 2010). Moreover, we anticipated that patterns of fruit morph production in relation to climate unpredictability should be stronger in *D. sinuata* which occurs in the more arid and climatically unpredictable Succulent Karoo biome, compared to *D. pluvialis* in the more mesic Cape Floristic Region occupied by *D. pluvialis*, but this was also not the case.

The strong allometric relationship between ray and disk florets indicates that constraints on inflorescence development may limit the ability of selection to alter relative allocation to dispersal and dormancy in this system. This could explain the mismatch between our data and theoretical expectations. However, perennial species, which are similarly allometrically constrained, did have significantly lower relative allocation to dormant fruit morphs than annuals, which suggests that selection can overcome developmental constraints. Another possibility, for which we do not have data, is that both fruit morph ratios and inflorescence size may have low heritability. Under this scenario, patterns of central vs. peripheral fruit production would likely reflect differences in the local pollinator environment and/or nutrient levels available to plants. For example, *D. pluvialis* sites with the highest rainfall unpredictability values predominantly occur along the West Coast and along the species' northern range edge into the Succulent Karoo biome and there is limited evidence to suggest that soil nutrient levels may vary among these regions and the Cape Floristic Region (Witkowski & Mitchell, 1987; Born *et al.*, 2007). Such local environmental factors may then obscure any broad spatial patterns. Finally, selection on the production of dispersive, non-dormant propagules vs. non-dispersive, dormant propagules may be exerted by factors other than temporal heterogeneity and range edge proximity (or at least the measures that we have used in our study). For example, the degree of autocorrelation in spatial and temporal environmental conditions is expected to influence patterns of covariation (Levin *et al.*, 1984; Cohen & Levin, 1991; Snyder, 2006; see Buoro & Carlson, 2014 for review).

Conclusions

Our study supports the theoretical predictions and previous empirical work suggesting that perennial species should invest relatively more in the production of dispersive fruit than annuals, but lack investment in dormant propagules. Annuals, on the other hand, produce high proportions of dormant propagules. In contrast, we find no support for the expectation that relative investment in dormancy should increase in annuals in climatically unpredictable sites. This could reflect a strong influence of local environmental factors on fruit production, obscuring the pattern among populations across broad climatic gradients (see Buoro & Carlson, 2014). On the other hand, studies of this nature are limited and do not consistently provide support for these theoretical predictions (e.g. Petru & Tielbörger, 2008; Siewert & Tielbörger, 2010). Our results point to the need for additional empirical tests of dispersal-dormancy theoretical predictions, particularly studies which simultaneously test for the influence of local determinants (e.g. pollen and resource availability) on fruit set, which could strongly influence the strength of selection to shape allocation patterns.

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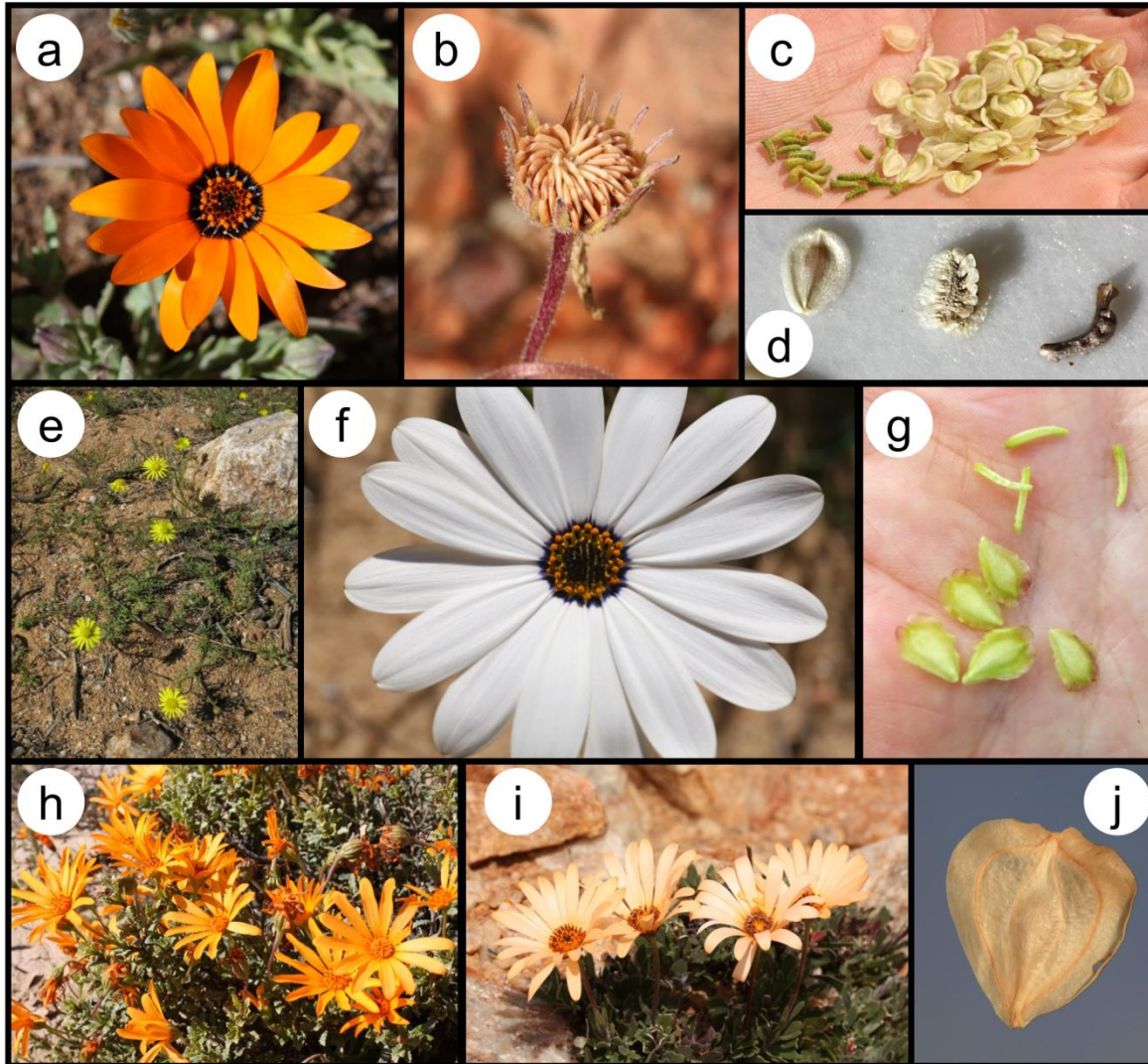


Fig. 4.1. Annual (a – f) and perennial (g – j) *Dimorphotheca* (Asteraceae) species from the Cape Floristic Region and Succulent Karoo Biome of South Africa and Namibia: (a) *D. sinuata* inflorescence; (b) mature *D. sinuata* infructescence; (c) immature peripheral (left) and central (right) achenes of *D. sinuata*; (d) mature central (left), winged peripheral (centre) and wingless peripheral (right) achenes of the trimorphic *D. polyptera*; (e) flowering *D. polyptera* plant; (f) *D. pluvialis* inflorescence; (g) immature central (bottom) and peripheral (top) achenes of *D. cuneata*; (h) *D. cuneata*; (i) *D. tragus*; (j) Mature *D. tragus* central achene.

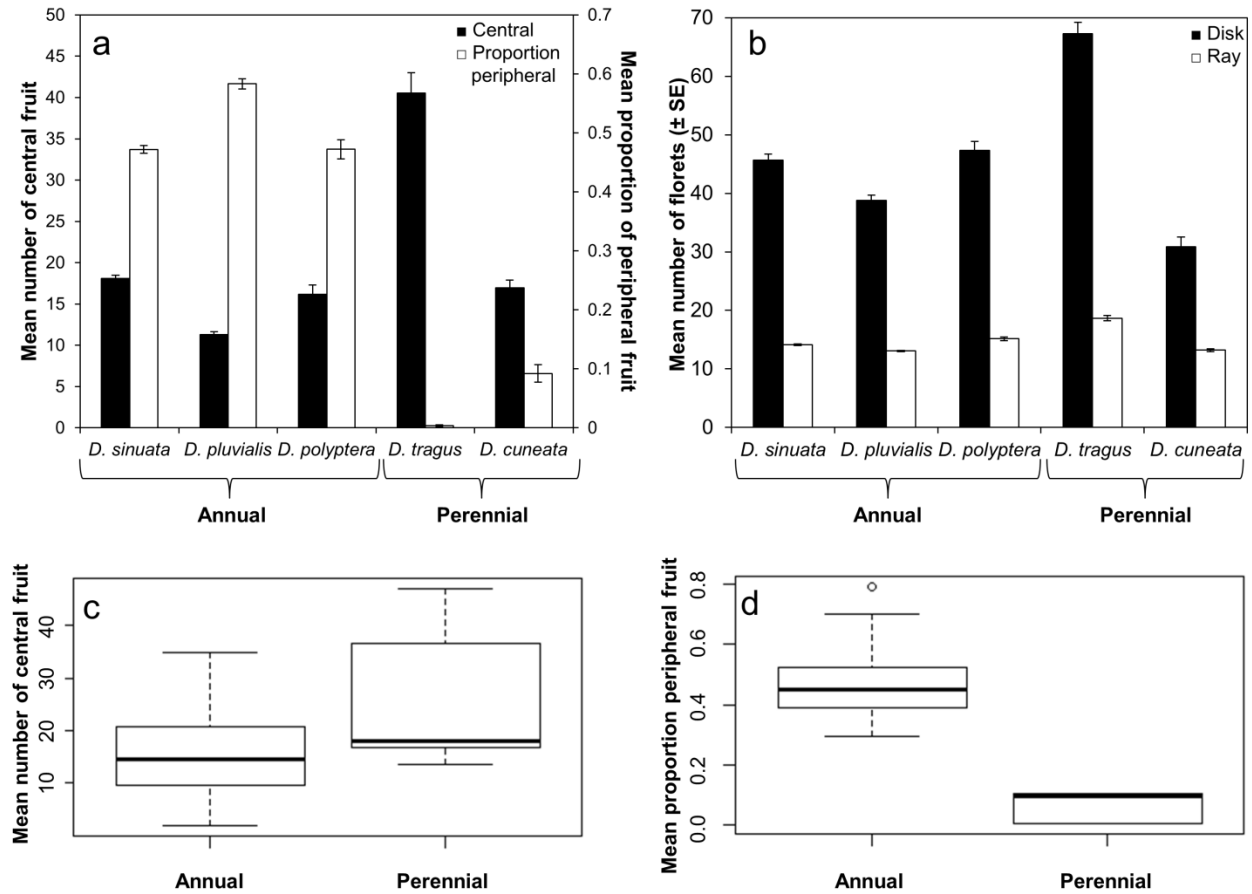


Fig. 4.2. (a) Mean (\pm SE) of central (i.e. dispersive) fruit and mean (\pm SE) proportion peripheral (i.e. dormant, non-dispersive) fruit and (b) mean numbers of disk (central) and ray (peripheral) florets for three annual and two perennial *Dimorphotheca* species from southern Africa; fitted estimates of (c) mean number of central fruit and (d) mean proportion of peripheral fruit in annuals and perennials from GLMMs (see text). Bold lines indicate the medians, boxes the interquartile range, whiskers the ranges and points are outliers.

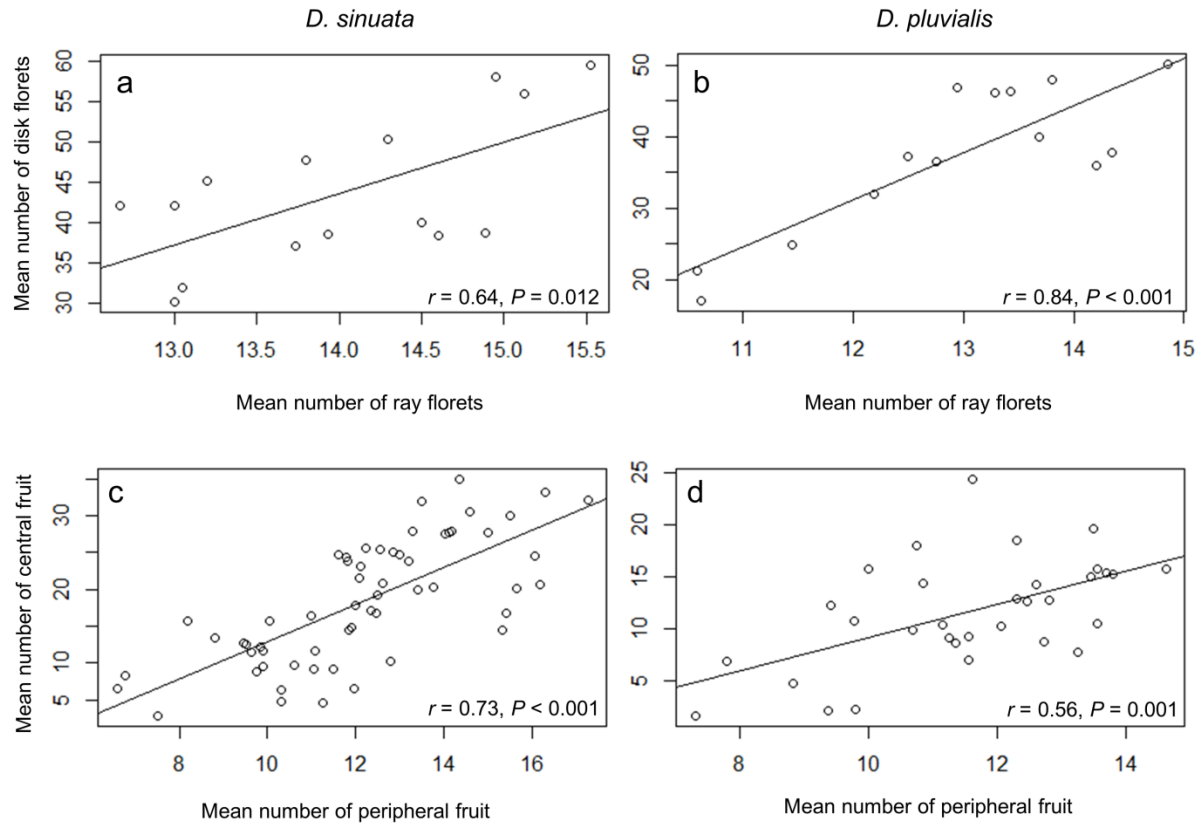


Fig. 4.3. Correlation of the mean number disk vs. ray florets and central vs. peripheral fruit in (a and c) *Dimorphotheca sinuata* and (b and d) *D. pluvialis*.

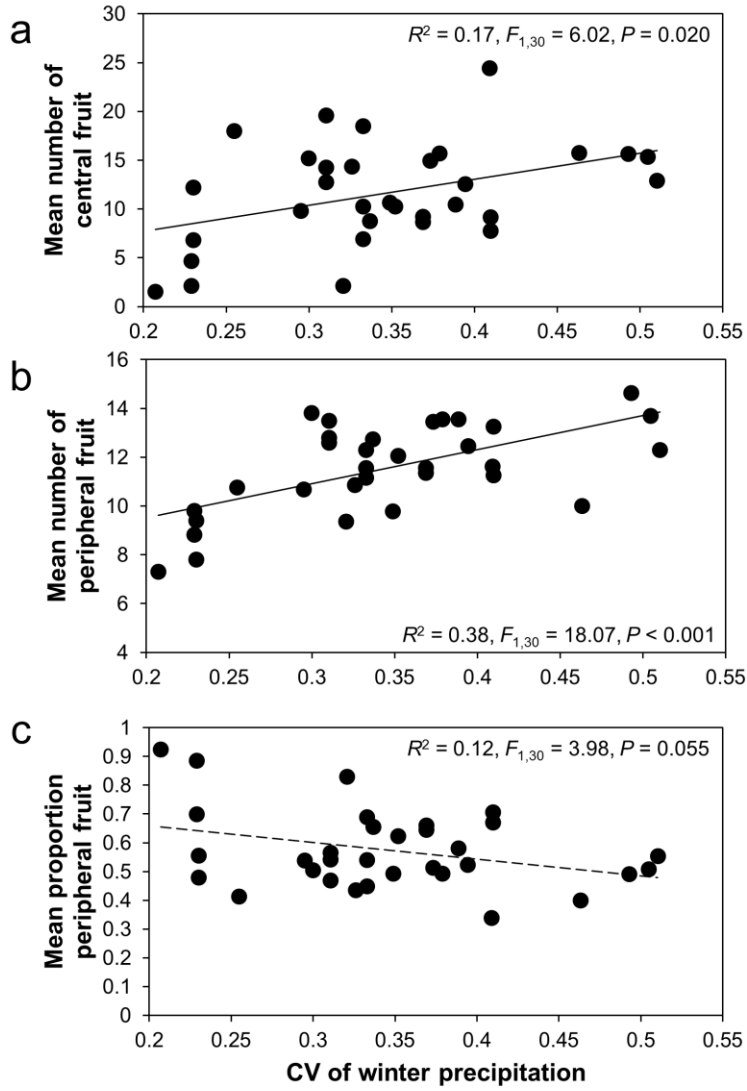


Fig. 4.4. Mean number of central fruit (a) and mean proportion peripheral fruit (b) in relation to the coefficient of variation (CV) of winter precipitation in populations of *Dimorphotheca pluvialis*.

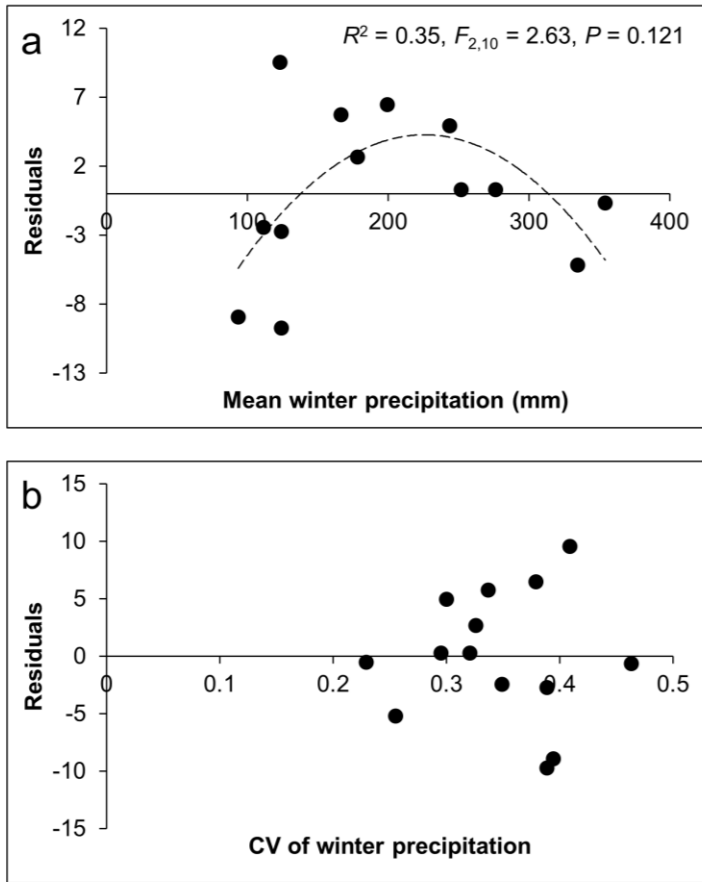


Fig. 4.5. Residuals of the disk-ray floret regression across populations of *Dimorphotheca pluvialis* in relation to (a) mean winter precipitation and (b) CV of winter precipitation. Positive residuals indicate more disk florets that expected, and vice versa, given the number of ray florets.

Chapter 5

**Dispersal-dormancy trade-offs at individual, population and species level in
annual and perennial southern African Asteraceae**

Abstract

Dispersal in space and in time are important risk-reducing strategies in unpredictable environments. Dispersal serves numerous functions, but also entails costs which can lead to trade-offs among traits that influence dispersal. Spatial and temporal dispersal are regarded as alternative risk-reducing strategies, and negative patterns of covariation between them are predicted at different levels of biological organisation. Moreover, these patterns may be affected by other life history traits that spread risk in time, e.g. iteroparity. Controlling for phylogeny, we found evidence for significant negative covariation between spatial dispersal (assessed from vertical fall time of fruits) and temporal dispersal (germination fractions) across 15 annual and 12 perennial wind-dispersed species in six Asteraceae genera from South Africa. Covariation patterns were consistent among annual and perennial species, suggesting that the trade-off does not depend on life history effects. Effects of life history on spatial and temporal dispersal were inconsistent. Annuals exhibited consistently higher dormancy compared to perennials. Fall time did not differ significantly among annual and perennial species, but was largely determined by evolutionary history. In seed heteromorphic species, individual fruit with adaptations for wind dispersal had significantly higher germination probabilities compared to unwinged fruit. In contrast, an individual-level trade-off between fall time and germination probability was not evident for species with monomorphic fruits. Similarly, evidence for trade-offs between spatial and temporal dispersal at the population-level was weak. Our findings suggest that dispersal and dormancy are important alternative risk-reducing strategies for southern African daisies, and that their relative importance is affected by iteroparity, which also spreads the risk of reproductive failure in time, and phylogenetic constraints. However, the nature of environmental heterogeneity (spatial vs. temporal) and the degree of environmental autocorrelation will also play a role. Our study provides novel empirical tests of predictions for trade-offs between seed dispersal and dormancy at different levels of biological organisation.

Introduction

Dispersal, the movement or transport of individuals away from their parents, is a key topic in the study of evolutionary and ecological processes (Levin *et al.*, 2003; Ronce, 2007; Clobert *et al.*, 2012). Dispersal can represent movement in space or movement in time, e.g. by dormant seeds, and considering its joint spatial and temporal dimensions is imperative in the context of life history evolution (Eriksson & Kiviniemi, 1999). Dispersal serves numerous functions, e.g. spreading risk among offspring, reducing kin competition and mating among relatives and escaping local unfavourable environments (reviewed in Matthysen, 2012; Duputié & Massol, 2013). However, the process of dispersal also carries costs, e.g. energetic costs associated with the development of morphological structures such as seed wings, risks associated with predation during the transfer stage, and risks that dispersing individuals arrive in unfavourable habitats (Bonte *et al.*, 2012; Travis *et al.*, 2012). Consequently, trade-offs can occur among traits that influence dispersal, because selection will act to maximise fitness and minimise overall costs (reviewed in Buoro & Carlson, 2014). In turn, these trade-offs can introduce patterns of covariation among morphological, behavioural and life-history traits that correlate with dispersal (dispersal syndromes; reviewed in Ronce & Clobert, 2012).

Dispersal in space and dispersal in time (e.g. dormancy) spread the risk associated with reproductive failure in heterogeneous and unpredictable environments. Because spatial and temporal dispersal both function as risk-reducing strategies, it is often predicted that they substitute for one another so that selection for one may constrain the evolution of the other (Venable and Lawlor 1980; Klinkhamer *et al.* 1987; Siewert and Tielbörger 2010; but see Snyder 2006). In a recent review of the relatively few studies that simultaneously investigated dispersal through space and time, Buoro and Carlson (2014) found that the majority of theoretical (i.e. modelling and simulation) studies reported evidence for a trade-off between the two strategies in unpredictable environments. In particular, the conclusions from these studies were that dispersal in space and time can evolve as alternative strategies in response to environmental heterogeneity and that selection for one strategy reduces selection for the other. Associations between dispersal in space and time can be studied at different levels of biological organisation (at the individual, population and species level); and negative relationships are predicted to emerge at each level

(reviewed in Buoro & Carlson, 2014). In contrast to theoretical expectations, the patterns of variation in spatial and temporal dispersal strategies are less uniform among empirical studies (also reviewed in Buoro & Carlson, 2014) and range from significant or weak negative covariation to more complicated patterns, or no relationship at all (e.g. Venable & Lawlor, 1980; Imbert, 1999; Bégin & Roff, 2002; Siewert & Tielbörger, 2010).

Covariation between spatial and temporal dispersal traits is also expected to be affected by the presence of other risk-reducing strategies. For example, by investing in longevity as survival strategy, iteroparous (reproducing more than once in a lifetime), perennial plants increase their probability of encountering favourable conditions for reproduction in time (Bulmer 1985; Ehrlén and Van Groenendael 1998; Zeineddine and Jansen 2009). Therefore, the need for other temporal dispersal strategies such as seed dormancy may be negated (Tuljapurkar, 1990; Rees, 1994). A few comparative studies have found evidence that dormant seed banks are associated with annuals rather than perennials (Rees, 1993, 1996; Thompson *et al.*, 1998). Growth habit can also influence spatial dispersal. For example, dispersal ability may be favoured in perennial plants to avoid kin competition and potential inbreeding (see Duputié & Massol, 2013). Indeed, in a comparative study of several thousands of species of Asteraceae, morphological adaptations for dispersal in space were significantly more prevalent among perennial than annual plants (Venable & Levin, 1983).

Here, we investigate spatial dispersal (propensity for wind dispersal) and two potential temporal dispersal strategies (seed dormancy and perennial growth habit) in wind-dispersed annual and perennial species across six genera of southern African Asteraceae. We examine covariation in seed dispersal and dormancy at different levels of biological organisation: individual, population and species level. We ask 1) Are there consistent differences in seed dispersal and dormancy among annual and perennial species?; 2) Is the probability of germination larger for more dispersive individual fruit?; 3) Is there evidence for the predicted trade-off (i.e. negative covariation) between seed dispersal and dormancy across populations within species?; 4) Is there evidence for a trade-off between dispersal and dormancy across species?; 5) Do patterns of covariation in seed dispersal and dormancy, if present, vary among annual and perennial species?

Materials and methods

Study species and sampling

Thirty-three annual and perennial Asteraceae species from six genera (Table S1) were sampled from their native distribution ranges in the winter-rainfall Greater Cape Floristic Region (Born *et al.*, 2007), South Africa. I focussed predominantly on the Namaqualand region of the arid Succulent Karoo biome (see Fig. S4.4), where environmental unpredictability may be expected to have large consequences for dispersal and dormancy in plants with different life history strategies. These species flower during late winter and spring (July – September) and produce achenes adapted for wind dispersal (Fig. 5.1). Sampling took place in August – September 2011-2013.

Dispersal measurements

We collected a bulk sample of mature fruits from at least five randomly chosen individuals per population for all species, except *Dimorphotheca* and *Osteospermum grandiflorum*. Four to 49 fruits (mean = 26.11 ± 6.95 SD), from 1-11 populations per species (mean = 4.15 ± 3.34 SD; total number of populations = 108), were randomly selected from each bulk sample and used for subsequent dispersal measurements (Table S1). For *Dimorphotheca* species and *O. grandiflorum*, which are seed heteromorphic, we collected mature seed families from 4-12 (mean = 9.27 ± 1.78 SD) randomly chosen individuals per population (Table S1). In *Dimorphotheca*, central fruit are adapted for wind dispersal, whereas peripheral fruit do not possess any adaptations for dispersal (see Chapter 4). *Osteospermum grandiflorum* individuals produce only peripheral fruit, but some possess wing-like appendages, presumably to aid wind dispersal. We selected approximately 3-5 achenes per morph per seed family in *D. sinuata*, *D. pluvialis*, *D. polyptera*, *D. cuneata* and *O. grandiflorum*. For *D. tragus*, only central fruit was sampled (as no mature peripheral fruit were found). For these seed heteromorphic species, fall time (see below) per morph per individual was determined from the mean values of these fruits.

To determine the relative wind-dispersal capacity of each population, we used a digital stopwatch to measure the time it took each fruit to fall to the ground when released at the top of a transparent Perspex tube (fall time). The tube measured 2.54 m in length and 0.21 m in diameter and was closed at the top except for a small hole in the centre through which fruits were released. The same observer recorded the time in each case. Fall time was obtained for each fruit as the average of three trials. For *Dimorphotheca* species and *O. grandiflorum*, population averages were adjusted according to the population fruit morph proportions (i.e. a weighted average) which varied significantly among populations (see Chapter 4). These adjusted values therefore reflect population-level dispersal averaged across all reproducing individuals in a population.

While we did not directly test whether fall time is proportional to dispersal distance in our study species, lateral movement of a wind-dispersed diaspore in a breeze is a function of the height of release, the wind velocity and the settling velocity, where a higher fall time corresponds to a lower settling velocity (Matlack, 1987; Greene & Johnson, 1992). Numerous studies have used fall time, settling velocity or rate of descent as proxy for dispersal distance in wind-dispersed plants (Matlack, 1987; Andersen, 1992; Cody & Overton, 1996; Fresnillo & Ehlers, 2008; see also De Waal *et al.*, 2014). Our measures of fall time are also significantly correlated to measures of wing loading (the ratio of mass to surface area of the fruit; Table S5.2). Wing loading has often been shown to be an accurate surrogate for dispersal distance, with a low wing loading corresponding to a greater dispersal distance (Augsburger, 1986; Augspurger & Franson, 1987; Matlack, 1987). Although our measure of dispersal ability need not necessarily translate to actual dispersal distances in the field due to the effects of e.g. height and structure of surrounding vegetation, wind speed, and height of the maternal plant, it allows us to rapidly compare at least one component of relative dispersal ability which would otherwise be impossible in the field (Andersen, 1992; Greene & Johnson, 1992).

Germination trials

To measure relative germination rates, 5-176 achenes (mean = 52.89 ± 37.56 SD) from 1-14 populations (mean = 5.08 ± 3.88 SD) of 26 species were placed on moist filter paper in petri dishes and incubated in a growth chamber at 20°C/10°C 14h/10h day-night cycle. Where

possible, for heteromorphic species fruit of different fruit morphs were included in these trials (see Table S5.1 for details). A total of 8003 fruit were used in these trials. Germination (protrusion of the radicle) was recorded daily for 30 days and the filter paper was moistened with distilled water as necessary. By the end of the experiment, ungerminated fruit were tested for viability as follows: the filter paper was moistened with a gibberellic acid solution (1g/L) to induce germination. Fruit that did not respond to this treatment were gently scarified with sand paper followed by re-application of the gibberellic solution. A small percentage of fruit (8.5%) did not germinate after any of these treatments, but were still considered viable because they remained firm and did not rot. Throughout the course of the germination trials, fruit that were soft and rotten or heavily covered by fungi were considered non-viable and removed from the trials (sensu Baskin & Baskin, 1998, p. 12). For each population we calculated the percentage dormant fruit (number of viable fruit that failed to germinate within 30 days/total number of viable fruit). The percentage dormant fruit for heteromorphic species were adjusted according to the population averages of morph proportions. In two populations for which morph proportions were not available, the species' averages of morph proportions were used to adjust germination percentages. As with adjusted fall time values, these adjusted dormancy values reflect the population (and species) dormancy capacity averaged across all individuals in a population.

Statistical analyses

Differences in dispersal and dormancy in annuals vs. perennials:

To compare differences of fall time in annual vs. perennial species, we used the average of species means (per life-history category) across six genera (15 annual and 18 perennial species for fall time; 16 annual and 12 perennial species for percentage dormant fruit). We ran one-sided paired t-tests (with the `t.test` function) to test the hypotheses that fall time should be higher and percentage dormant fruit should be lower in perennials compared to annuals.

To investigate the effects of genus and life history on fall time, a linear mixed effects model was run using the function `lmer` in the package `lme4` (Bates *et al.*, 2013). Genus, life history and the genus \times life history interaction were entered as fixed factors. Population nested within species nested within genus was included as random factor. The model was fitted by

maximum likelihood (ML) and was not overdispersed. Significance of factors was estimated by comparing models in which the factor of interest was dropped to the full model, using the function `anova`.

The effect of genus and life history on the proportion dormant fruit (the proportion of fruit per population that did not germinate within the 30 day germination trial) was analysed using a generalised linear mixed effects model with a binomial distribution using the function `glmer` in the package `lme4` (Bates *et al.*, 2013). Genus, life history and the genus \times life history interaction were treated as fixed factors. Species nested within genus was entered as a random factor. The model was overdispersed; consequently observation-level variability was also included as random factor. Significance of fixed effects was estimated as described above. Because no fruit germinated in any populations of *Arctotis* spp., causing numerical problems in the analysis, the proportion dormant fruit per population was calculated from (number of fruit that germinated + 1) and (number of fruit that failed to germinate + 1).

Individual-level trade-offs between dispersal and dormancy:

To test for relationships between fall time and dormancy within populations of monomorphic species (individual-level), in 2-3 populations of 12 species where fall time and germination of individual fruits were measured, we used two approaches. First, we analysed dormancy as a categorical dependent variable, where each fruit did or did not germinate within the 30-day germination trial, using logistic regression (binomial glm), i.e. asking whether the probability of germination was higher for more dispersive fruit, in 20 populations of 11 species. Second, dormancy was analysed as continuous count variable, calculated as [30 – days to germination] for each individual fruit, with fall time as predictor variable within eight populations of six species, with the `glm.nb` function in the `MASS` package (Venables & Ripley, 2002). Models were fit with a negative binomial distribution and a log link function. We also ran models with the `zeroinfl` function (Zeileis *et al.*, 2008) in the `pscl` package (Jackman, 2012) to account for zero-inflation. To determine whether the zero-inflated model was superior to the negative binomial model, we used Vuong's non-nested hypothesis test with the `vuong` function (Vuong, 1989). Results of these analyses were similar to those of the binomial glm and we report them in Table S5.3.

We also tested for individual-level trade-offs between dispersal and dormancy in seed heteromorphic *Dimorphotheca* species. In the dimorphic *D. sinuata* and *D. pluvialis*, fall time of central (winged) and peripheral (unwinged) fruit portrayed a clear bimodal pattern (C. de Waal, unpublished results). Similarly, fall time varied significantly between winged central, winged peripheral and unwinged peripheral fruit in the trimorphic *D. polyptera* (C. de Waal, unpublished results). Consequently, to test for individual-level trade-offs between seed dispersal and dormancy in these species, we conducted binomial glms with dormancy as a binomial response variable (did or did not germinate within the 30 day germination trial) and dispersal as categorical predictor variable (winged vs. unwinged fruit in 15 *D. sinuata* and 11 *D. pluvialis* populations, or winged central vs. winged peripheral vs. unwinged peripheral in 5 *D. polyptera* populations).

Population-level trade-offs between dispersal and dormancy:

To test for relationships within species between the mean fall time and the percentage dormant fruit (population-level), we conducted correlations for species from which we had obtained both measurements from at least six populations. We conducted tests on seven species in total. If both variables were representative of a normal distribution, we conducted Pearson's product moment correlations with the `cor.test` function. In two cases (*O. amplexans* and *O. hyoseroides*), the percentage dormant fruit was arcsine square-root transformed. In two cases (*O. oppositifolium* and *O. monstrosum*), applying a transformation did not improve normality of the data; consequently a non-parametric Spearman rank test was conducted. To determine whether the slopes of these relationships differ significantly from 0, we performed a one sample t-test. We also tested for a relationship between population means of fall time (response variable) and percentage dormant fruit (predictor variable) across all 115 populations. To control for variation associated with phylogenetic relatedness, we included the effects of genus and species nested within genus as random factors. This analysis was performed with the `lmer` function in `lme4` (Bates *et al.*, 2013).

Species-level trade-offs between dispersal and dormancy:

To test for relationships between fall time and percentage dormant fruit across species (27 species for which we had both dispersal and dormancy measures), linear regressions (with the `lm`

function) were performed using species means 1) across all species, 2) across annual species only, and 3) across perennial species only. Residuals were normally distributed and exhibited no patterns in relation to fitted values.

We tested for phylogenetic signal in fall time and percentage dormant fruit across species. A phylogeny for the 27 species was pruned from trees in Panero and Funk (2008) and Funk and Chan (2008). Within genera, relationships between species were left unresolved except in *Ursinia*, in which two subgenera are recognised (Prassler, 1967; Swelankomo, 2008). Branch lengths were set to one. To test for the presence of phylogenetic structure in fall time and percentage dormant fruit, we conducted Abouheif's C_{mean} tests (Abouheif, 1999; Münkemüller *et al.*, 2012) using the function `abouheif.moran` in the package `adephylo`. The matrix of phylogenetic proximities was obtained with the function `proxTips` and method `oriAbouheif` (Jombart & Dray, 2008). Fall time displayed phylogenetic structure (Abouheif's C_{mean} tests; $P = 0.001$), although no phylogenetic signal was apparent for percentage dormant fruit ($P = 0.133$). Consequently, we used a phylogenetic least squares (PGLS) analysis to assess the relationship between fall time and percentage dormant seeds across all species. We assumed a Brownian motion model of evolution and obtained the phylogenetic correlation structure using the function `corBrownian` in the package `ape` (Paradis *et al.*, 2013). The PGLS regression was run using the function `gls` in the `nlme` package (Pinheiro *et al.*, 2014). Fall time was entered as the dependent variable, with percentage dormant fruit as effect. The residuals were normally distributed and exhibited no patterns with respect to fitted values or the predictor variable. When percentage dormant fruit was entered as dependent variable, results were similar but assumptions were no longer met. The PGLS regression with the hypothesised phylogeny was compared to a model with a star phylogeny in which all relationships were left unresolved (equivalent to an ordinary least squares regression). Pagel's λ (Pagel, 1999), which indicates the extent to which species differences are predicted by phylogeny assuming a Brownian process, was 1.08 for the regression of fall time vs. percentage dormant fruit, further supporting our use of a PGLS approach.

Results

Dispersal and dormancy in annual vs. perennial species

There was no consistent trend of higher fall time in perennials compared to annuals in six genera (Fig. 5.2a; Fig. S5.1; one-sided paired t-test, $t = -1.28$, $df = 5$, $P = 0.128$). Fall time was significantly affected by genus identity ($X^2 = 47.32$, $df = 5$, $P < 0.001$) but not by life history ($X^2 = 0.94$, $df = 1$, $P = 0.332$). Neither was there evidence for a genus \times life history interaction ($X^2 = 4.19$, $df = 5$, $P = 0.523$).

Consistently more fruit from annual species failed to germinate within 30 days compared to perennials (Fig. 5.2b; Fig. S5.2; $t = 2.41$, $df = 5$, $P = 0.030$). The proportion dormant fruit in six genera was significantly affected by genus identity ($X^2 = 19.29$, $df = 5$, $P = 0.002$), and life history ($X^2 = 14.69$, $df = 1$, $P < 0.001$). However, the genus \times life history interaction was also significant ($X^2 = 14.31$, $df = 5$, $P = 0.014$), although this interaction seemed to be driven by a single genus, *Ursinia* (Fig. 5.2b).

Individual-level (within population) trade-offs between fall time and dormancy

We did not detect trade-offs between fall time and dormancy within individuals of monomorphic species. Apart from a marginally significantly higher probability of germination for more dispersive fruit in the *O. hyoseroides* population Wphoek ($z = 1.73$; $P = 0.083$), no patterns were evident within 19 populations of 11 species (Table 5.1).

In seed heteromorphic species of *Dimorphotheca*, individual-level trade-offs in fall time and dormancy were evident. The probability of germination was significantly higher for winged fruit compared to unwinged fruit in 12 of 15 *D. sinuata* populations and 10 of 11 *D. pluvialis* populations (Table 5.2). In the three non-significant *D. sinuata* populations (Klawer, Piket1 and Richtersveld), the probability of germination was low for any fruit, regardless of morph (0.07, 0.07 and 0.17, respectively). In the non-significant *D. pluvialis* population (Agulhas), germination was spread evenly among fruit morphs. In *D. polyptera*, the probability of

germination in winged peripheral vs. unwinged peripheral fruit was equally low, but in three of the five populations, the probability of germination of winged central fruit was significantly higher than unwinged peripheral fruit (Table 5.2). In KhubLek4 and RoshPina4, the probability of germination was low overall, regardless of fruit morph (0.11 and 0.13, respectively).

Intraspecific (population-level) trade-offs between fall time and dormancy

Of the seven species tested, only two species (*O. hyoseroides* and *O. amplexens*) exhibited marginally significant relationships between fall time and percentage dormant fruit of populations, but the associations were in opposite directions ($r = -0.63$, $P = 0.068$ and $r = 0.62$, $P = 0.054$, respectively; Fig. 5.3). Across all seven species, three showed positive trends between dispersal and dormancy and four showed negative trends (Fig. 5.3). These slopes did not differ significantly from 0 ($t = -0.87$, $df = 6$, $P = 0.416$). Across all populations ($n = 115$), there was no relationship between dispersal and dormancy, when controlling for the effects of genus and species ($X^2 = 1.24$, $df = 1$, $P = 0.265$).

Species level (interspecific) trade-offs between dispersal and dormancy

Fall time was negatively associated with the percentage dormant fruit across all species (Fig. 5.4a; $R^2 = 0.19$, $F_{1,25} = 5.68$, $P = 0.025$) and across annual species (Fig. 5.4b; $R^2 = 0.36$, $F_{1,23} = 7.44$, $P = 0.017$). Across perennial species the pattern was marginally non-significant (Fig. 5.4c; $R^2 = 0.25$, $F_{1,10} = 3.38$, $P = 0.096$).

Accounting for phylogenetic relatedness, a significantly negative association was still evident between fall time and percentage dormant fruit across species (Fig. 4a; $\beta = -0.01$, $t_{27} = -2.63$, $P = 0.014$). The model incorporating the hypothesised phylogeny was superior ($\Delta AIC = 18$) to a model with a star phylogeny (equivalent to the OLS regression; $\beta = -0.01$, $t_{27} = -2.38$, $P = 0.025$). A PGLS regression was marginally non-significant across annual species (Fig. 5.4b; $\beta = -0.01$, $t_{15} = -1.80$, $P = 0.095$) and significant across perennial species (Fig. 5.4c; $\beta = -0.01$, $t_{12} = -2.24$, $P = 0.049$). Both of these models were also superior to those where phylogenetic relationships were left unresolved ($\Delta AIC = 4$ and 2 , respectively).

Discussion

Influence of life history on dispersal in space and time

The effects of life history (annual or perennial growth habit) on spatial and temporal dispersal were not consistent in our study of 33 South African Asteraceae. Life history strongly affected dormancy of our study species. Annual species consistently displayed higher delayed germination compared to perennial species (Fig. 5.2b) and no phylogenetic signal in the percentage dormant fruit was detected. These findings are consistent with a negative trade-off between dormancy and longevity as alternative strategies to spread risk of reproductive failure in time (Tuljapurkar, 1990; Rees, 1993, 1994). In addition, the importance of delayed germination as bet-hedging strategy for annual plants, especially in arid environments, is well documented (e.g. Venable, 2007; Gremer & Venable, 2014). In contrast, fall time did not consistently differ between annual and perennial species (Fig. 5.2a), indicating that dispersal ability was strongly affected by evolutionary history. This was corroborated by a strong phylogenetic signal in fall time.

Covariation between seed dispersal and dormancy

A significant negative relationship between dispersal and dormancy was evident across our 27 study species, even when accounting for phylogenetic relatedness among taxa (Fig. 5.4a). The negative relationship between fall time and dormancy persisted within life history categories (Fig. 5.4a-c), suggesting that the pattern is not simply a result of life history evolution, or driven by traits linked to life history (e.g. low dormancy in perennials). These findings are consistent with the predicted negative pattern of covariation of dispersal in time and space at the species level (reviewed in Buoro & Carlson, 2014). In a comparative study across 171 species of British plants, using phylogenetic independent contrasts, species with less seed dormancy were more likely to possess efficient seed dispersal strategies (Rees, 1993). Similarly, in a study of Swedish herbs and grasses (Eriksson, 1996), species predominantly exhibited means to disperse in time (e.g. seed banks), but lacked features that allowed dispersal in space (e.g. fleshy fruits, adhesive or wind dispersal). Although both of these studies indicate the presence of a trade-off, they did

not investigate covariation between dispersal ability and dormancy. Moreover, these studies relied on the classification of seed dispersal as a discrete variable, according to the presence/absence of morphological traits. In contrast, we measured fall time and wing loading as surrogates for dispersal ability, allowing us to uncover variation in dispersal ability among species that are all morphologically adapted for wind dispersal. Although our method to quantify dispersal (fall time) may overestimate the importance of dispersal altogether (see Siewert & Tielbörger, 2010), we applied it to members of the same plant family with the same dispersal syndrome. In addition, the strong species-level variation in dispersal suggests that our method is valid.

Although we detected significant negative species-level covariation between spatial and temporal dispersal, we found weak evidence for these patterns at the population-level. Of the seven species we investigated (six annual and one perennial species), only two closely related annuals (*Osteospermum hyoseroides* and *O. amplectens*) exhibited marginally significant trends, but in opposite directions (Fig. 5.3 c-d). Moreover, the slopes of patterns were not in a consistent direction (Fig. 5.3a). Our study provides a much needed empirical investigation of covariation in dispersal and dormancy among plant populations, since, to our knowledge, only two empirical studies exist that have addressed this question. In the first of these studies, Siewert & Tielbörger (2010) also found weak evidence for trade-offs among populations that occurred across a gradient of environmental unpredictability in Israel. They attributed their findings to their study species' extremely low investment in dispersal compared to dormancy and local reproduction. Our results contradict a study by Gravuer *et al.* (2003) which found evidence of a negative relationship between dispersal capability and germination success among populations of *Liatris scariosa* (Asteraceae). They also found that this trade-off was relatively consistent across populations in different environments.

At the individual-level, we found a dichotomy between seed heteromorphic and monomorphic species. In seed heteromorphic *D. sinuata*, *D. pluvialis* and *D. polyptera*, fruit that possessed attributes that facilitate wind dispersal (i.e. winged, central fruit) were significantly more likely to germinate during the course of our germination trial. This is in line with other studies of seed heteromorphic plants that have also shown the existence of such a trade-off

within seeds (e.g. Venable & Lawlor, 1980; McEvoy, 1984; Imbert, 1999). Individual-level trade-offs are usually predicted as the result of biophysical constraints (e.g. physiological trade-offs; Buoro & Carlson, 2014). For example, the production of wings for wind dispersal ability and the production of thick pericarps or chemical germination inhibitors may compete for the same limiting resources. Alternatively, weight constraints may cause dispersability to be traded off against seed size (Venable & Brown, 1988) or pericarp thickness.

However, in monomorphic species we did not detect low germination probabilities in less dispersive fruit, at least for the measures of spatial and temporal dispersal that we used, except for a weak trend in a single population of *O. hyoseroides*. We also did not detect population-level patterns of covariation in any of the seven species we investigated, suggesting evolutionary constraints on responding to selection imposed by both spatial and temporal heterogeneity. Poor relationships between spatial and temporal dispersal may be expected if variation in resource availability or variation in resource acquisition occur among microsites inhabited by individuals, or across sites. For example, trade-off patterns may be obscured when some individuals have nearly unlimited nutrients to invest in both dispersal and dormancy, while others have few resources to invest in only one strategy (Van Noordwijk & De Jong, 1986; Buoro & Carlson, 2014). Alternatively, the degree of environmental autocorrelation may influence patterns of covariation (where positive autocorrelation occurs when conditions in the current site or temporal period resemble conditions in a nearby site or the previous period). For example, both strategies can be favoured when spatial and temporal autocorrelation are negative or weak, or selected against when spatial and temporal autocorrelation are both positive (Levin *et al.*, 1984; Venable & Brown, 1988; Cohen & Levin, 1991; Snyder, 2006).

Nevertheless, we did find evidence for individual-level trade-offs in *Dimorphotheca* as well as negative covariation between dispersal and dormancy on the species level. This may be likely if dispersal in space and time evolve in response to different selection pressures. Indeed, recent studies suggest that dispersal and dormancy cannot substitute for each other as alternative risk-reducing strategies in unpredictable environments (Snyder, 2006; Siewert & Tielbörger, 2010; Vitalis *et al.*, 2013). Although dormancy may evolve in response to climatic (i.e. temporal) unpredictability (Cohen, 1966), dispersal is more likely to evolve in response to e.g. kin

competition or selection for colonisation, or as adaptive response to predictably deteriorating environments, such as during succession (Levin *et al.*, 1984; McPeck & Holt, 1992; Imbert & Ronce, 2001; Ronce, 2007; Vitalis *et al.*, 2013). Knowledge of the type of seed dormancy and germination ecology of our study species, as well as environmental autocorrelation across their distribution ranges, may be necessary to explain the mismatch between theoretical expectations and our results.

Conclusions

Our study provides a novel contribution in the form of empirical tests of patterns of variation in spatial and temporal dispersal predicted by theory, by simultaneously testing for the hypothesised negative relationship at different levels of biological organisation. We show that the effects of life history on dispersal in space and time are not consistent. As expected, dormancy is traded off against longevity. However, wind dispersal ability is strongly determined by evolutionary history. We found evidence for trade-offs between spatial and temporal dispersal within fruit in heteromorphic species, but not in monomorphic species. Also, evidence for population-level covariation was weak. In contrast, across all species, and across species within different life history categories, a trade-off between dispersal in space and time was evident, suggesting that the pattern is not only driven by life history effects. Spatial and temporal dispersal as alternative risk-reducing strategies have important consequences for population dynamics and species persistence (Eriksson, 1996; Duputié & Massol, 2013; see Buoro & Carlson, 2014 for review), underscoring the need for further studies that integrate risk-spreading trade-offs and improve our understanding of the causes, consequences and constraints on their evolution.

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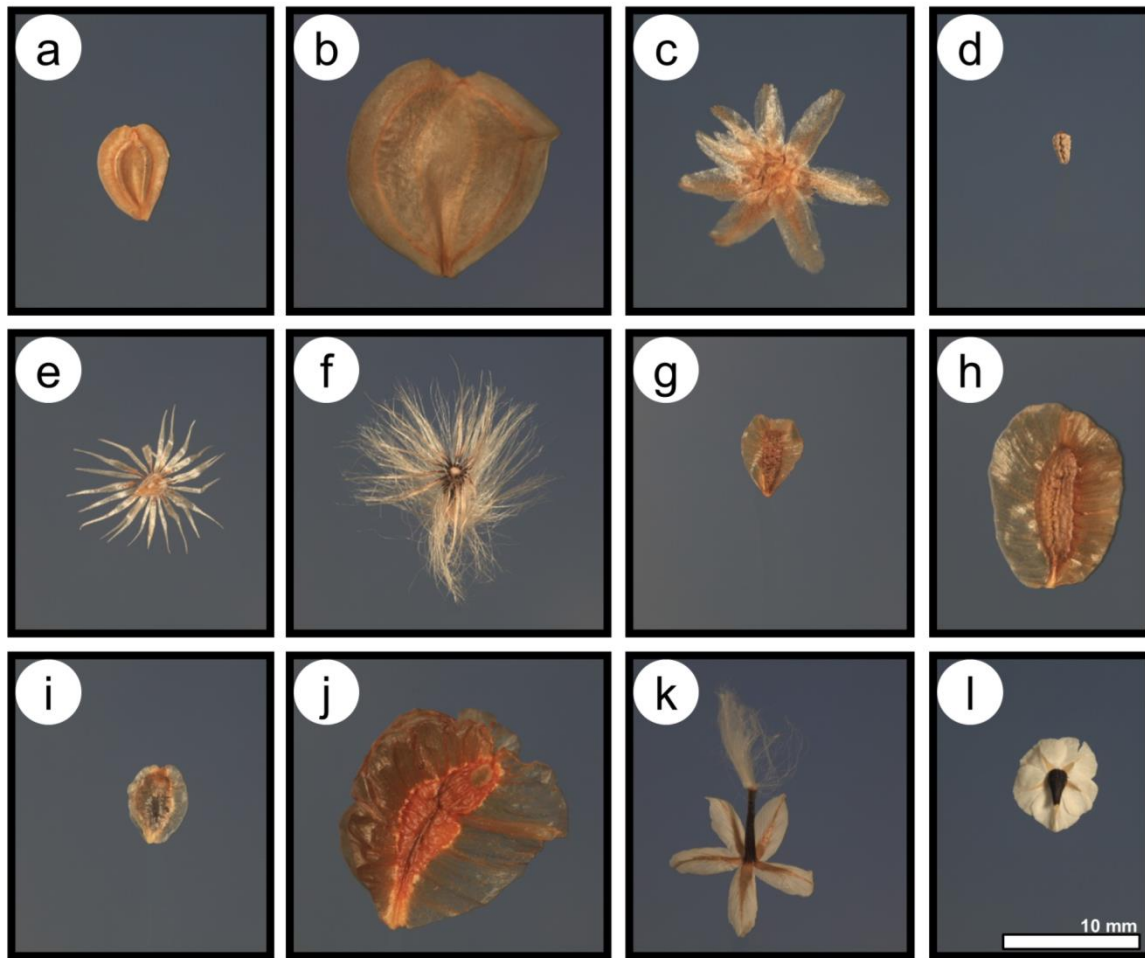


Fig. 5.1. Representative samples of mature fruit of annual (an) and perennial (p) southern African Asteraceae. (a) *Dimorphotheca sinuata* (an), (b) *D. cuneata* (p), (c) *Arctotis acaulis* (p), (d) *A. fastuosa* (an), (e) *Gazania tenuifolia* (an), (f) *G. pectinata* (p), (g) *Osteospermum amplectens* (an), (h) *O. monstrosum* (an), (i) *O. microcarpum* (an), (j) *O. sinuatum* (p), (k) *Ursinia anthemoides* (an), (l) *U. cakilefolia* (an).

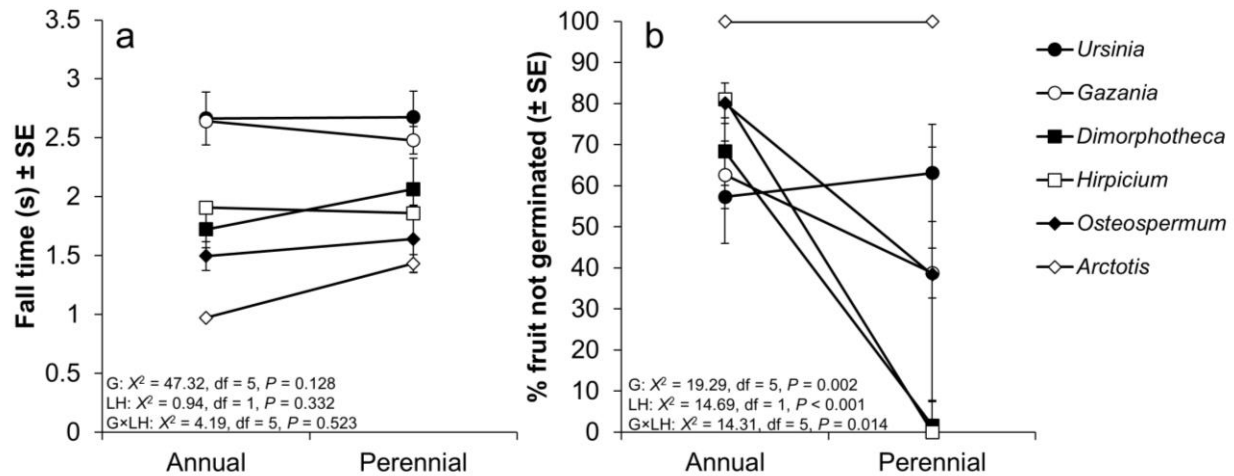


Fig. 5.2. (a) Mean fall time (\pm SE) and (b) mean percentage fruit not germinated within 30 days of annual and perennial taxa in six genera of southern African Asteraceae. High fall time values and high percentage ungerminated fruit represent high dispersal ability and high dormancy, respectively. Results of generalised linear mixed models are indicated for the effects of genus (G), life history (LH) and the genus \times life history (G \times LH) interaction. In dimorphic taxa (*Dimorphantheca* and *Osteospermum grandiflorum*) fall time averages and germination percentages were adjusted for the relative morph proportions in populations (see text).

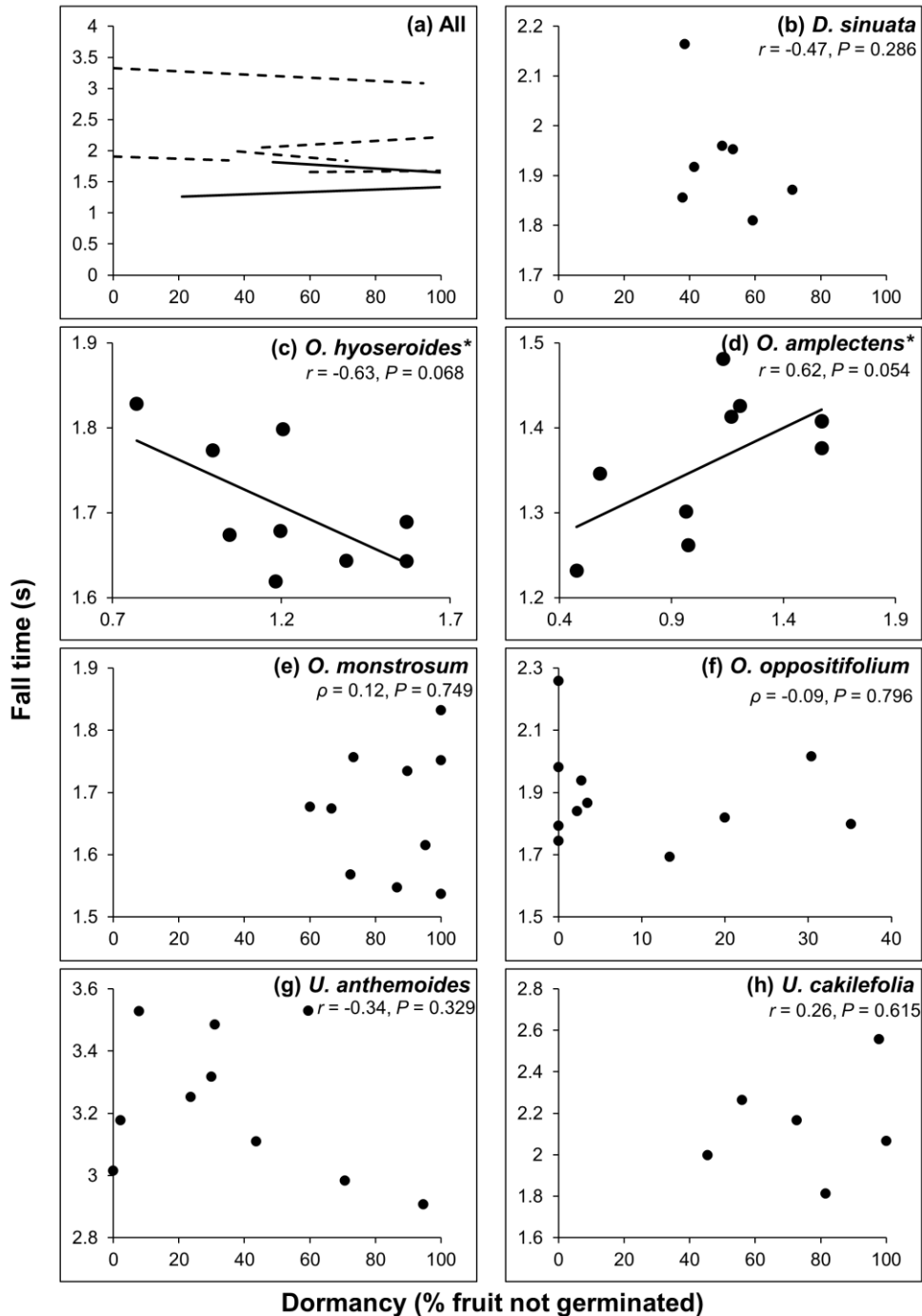


Fig. 5.3. Relationships between mean fall time and percentage dormant fruit across populations of seven Asteraceae species. (a) Slopes of marginally non-significant (solid lines) and non-significant (dashed lines) trends between dispersal and dormancy of all seven species and (b – h) relationships among populations within each species are shown. Test statistics are r for Pearson's product moment correlations and ρ for Spearman rank tests (non-parametric). * Percentage dormant fruit was arcsine square-root transformed in *O. hyoseroides* and *O. amplexens*.

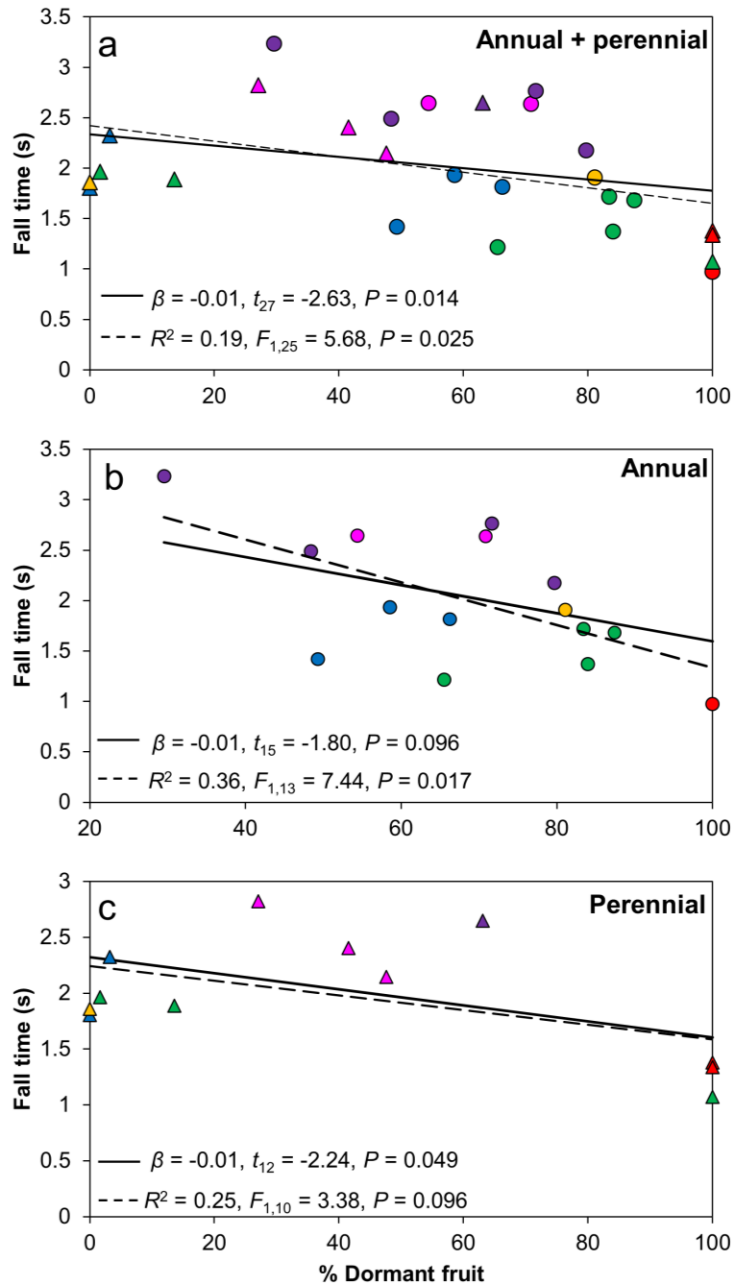


Fig. 5.4. Relationships between species means of fall time and percentage dormant fruit of annual (circles) and perennial (triangles) species in six genera of southern African Asteraceae (*Arctotis* (red), *Dimorphotheca* (blue), *Gazania* (pink), *Hirpicium* (orange), *Osteospermum* (green), *Ursinia* (purple)) shown (a) across all species, (b) across annual species only, and (c) across perennial species only. The regression models taking hypothesised phylogenetic relationships into account (solid lines) were superior to models assuming a star phylogeny (dashed lines; equivalent to ordinary linear regressions).

Table 5.1. Results of logistic regression (binomial glm) to test whether the probability of germination is larger for more dispersive fruit, in populations of 11 annual and perennial species of southern African Asteraceae.

| Species | Population | <i>z</i> | <i>P</i> |
|------------------------------|-------------------|-----------------|-----------------|
| <i>Gazania tenuifolia</i> | GrasEk | -1.25 | 0.210 |
| | Oranjevallei3 | -0.10 | 0.924 |
| <i>O. amplexans</i> | Vonkel | 0.002 | 0.999 |
| | Kamies | -0.88 | 0.381 |
| <i>O. hyoseroides</i> | Kamies | 1.44 | 0.151 |
| | Wphoek | 1.73 | 0.083 |
| <i>O. microcarpum</i> | VanNie2 | 1.36 | 0.175 |
| | Hond5 | -1.53 | 0.127 |
| | GrasEk | 0.28 | 0.783 |
| <i>O. monstrosum</i> | VanNie1 | 0.69 | 0.492 |
| <i>O. oppositifolium</i> | Lutzville | -0.13 | 0.895 |
| <i>U. anthemoides</i> | Spektakel | -0.81 | 0.417 |
| | Graaf | 1.22 | 0.221 |
| <i>U. cakilefolia</i> | Skilpad | 1.24 | 0.216 |
| | Karkhams | 0.25 | 0.804 |
| <i>U. calenduliflora</i> | Spektakel | -0.91 | 0.365 |
| | Okiep2 | -0.63 | 0.531 |
| <i>U. nana</i> | EksRd1 | 1.05 | 0.293 |
| <i>Ursinia</i> perennial sp. | CalGarContact | -0.12 | 0.904 |
| | Studerspess2 | 0.18 | 0.855 |

Table 5.2. Results of binomial generalised linear models to test whether the probability of germination is higher for central, winged (dispersive) fruit compared to peripheral, unwinged (non-dispersive) fruit in the dimorphic *Dimorphotheca sinuata* and *D. pluvialis*. In the trimorphic *D. polyptera* the probability of germination for central, winged (CW) and peripheral, winged (PW) fruit was tested against peripheral, unwinged fruit as reference.

| Species | Pop | z | P |
|---------------------|---------------------|-----------------------|-----------------------|
| <i>D. sinuata</i> | VanClan3 | 2.29 | 0.022 |
| | Stein | 3.29 | 0.001 |
| | Springbok | 5.24 | < 0.001 |
| | Lamberts | 3.91 | < 0.001 |
| | Klip | 3.99 | < 0.001 |
| | Kamies | 4.06 | < 0.001 |
| | Kamberg | 5.27 | < 0.001 |
| | EkLek4 | 3.45 | 0.001 |
| | Bulletrap | 4.30 | < 0.001 |
| | Moedverloor | 2.78 | 0.005 |
| | Richtersveld | 0.96 | 0.337 |
| | Piket1 | 0.73 | 0.469 |
| | Steinkoppie | 4.10 | < 0.001 |
| | Kliprand1 | 5.47 | < 0.001 |
| | Klawer | 1.24 | 0.215 |
| <i>D. pluvialis</i> | VanClan1 | 4.74 | < 0.001 |
| | PNStein1 | 2.93 | 0.003 |
| | Varsch | 5.79 | < 0.001 |
| | Avontuur | 5.80 | < 0.001 |
| | Eendekuil | 3.69 | < 0.001 |
| | Hope1 | 3.95 | < 0.001 |
| | Tokai | 5.07 | < 0.001 |
| | Pearly Beach | 5.01 | < 0.001 |
| | Velddrif | 6.08 | < 0.001 |
| | Lamberts | 5.68 | < 0.001 |
| | Agulhas | 1.12 | 0.264 |
| | <i>D. polyptera</i> | Site1 | CW: 3.57 PW: -0.28 |
| Platbakkies | | CW: 2.96 PW: -0.33 | 0.003 0.742 |
| Suurdam | | CW: 6.39 PW: -0.38 | < 0.001 0.703 |
| RoshPina4 | | CW: 1.55 PW: -0.35 | 0.122 0.730 |
| KhubLek4 | | CW: 1.12 PW: 0.60 | 0.265 0.550 |

Chapter 6

Conclusions

All natural environments are characterised by spatial and temporal heterogeneity. Moreover, environments are expected to become increasingly unpredictable as a consequence of global climate change. In my dissertation, I have explored multiple strategies that allow plants to spread their risk in space (seed dispersal) and time (dormancy and perenniality), as well as reduce their risk in unfavourable/unreliable pollinator environments (breeding system). My research demonstrates that interactions between dispersal, dormancy and breeding systems in the context of life history, geographic position and climatic unpredictability are clearly complex and often contradict theoretical expectations.

My findings support the existence of two discrete syndromes among annual South African daisies: high selfing ability associated with good dispersal and obligate outcrossing associated with lower dispersal ability. This is consistent with the hypothesis that selection for colonisation success drives the evolution of an association between these traits. However, no general effect of range position on breeding system or dispersal traits was evident. This suggests selection on both breeding system and dispersal traits act consistently across these species' distribution ranges. Selfing ability has probably evolved in tandem with dispersal ability, most likely because autogamy offers reproductive assurance to dispersal-prone individuals that are more likely to experience conditions of pollen limitation, regardless of range position.

I also did not detect an effect of range position on relative investment in dispersal vs. dormancy in seed heteromorphic, annual *Dimorphotheca* species. Moreover, I found no support for the expectation that bet-hedging through relative investment in dormancy should increase in climatically unpredictable sites. This could reflect a strong influence of other local environmental factors on fruit production (for example variation in soil nutrient availability or pollinator environment), obscuring the pattern among populations across broad geographic

gradients. Alternatively, selection on the production of dispersive, non-dormant propagules vs. non-dispersive, dormant propagules may be exerted by factors other than temporal heterogeneity and range edge proximity.

Interestingly, I show that the effect of life history strategy on dispersal and dormancy is not consistent. Longevity is an alternative temporal risk-reducing strategy and therefore theory predicts that it negates the need for dormancy. In support of this, I found that perennials tended to produce few dormant propagules and that annuals tended to produce many. In annuals, the importance of delayed germination as bet-hedging strategy, especially in arid environments, is well documented. Dispersal on the other hand was more strongly affected by phylogenetic relatedness than by life history. For example, perennial *Dimorphotheca* invested more in the production of dispersive fruit compared to annuals, which supports the prediction that dispersal is favoured in perennial plants to avoid kin competition, to increase the probability of recruitment of scarce sites or to operate as alternative risk-reducing strategy to dormancy. However, I show that this pattern is not consistent across different genera, indicating the presence of phylogenetic structure in traits that affect wind dispersal ability.

Across 27 daisy species, controlling for phylogeny, I found evidence for negative covariation between dispersal and dormancy. Moreover, this pattern was consistent across annual vs. perennial species, suggesting that it is not only driven by life history effects. This is consistent with the prediction for a trade-off between traits that affect dispersal and dormancy. Negative covariation between dispersal and dormancy of different species in the same environment may reflect interactions between a temporal storage effect and a spatial storage effect (e.g. involving competition-colonisation trade-offs) (Chesson, 2000a; b; Snyder & Chesson, 2004; Facelli *et al.*, 2005), which can facilitate coexistence of multiple species when individual species respond differently to environmental variation (Buoro & Carlson, 2014). However, in contrast to expectations, I show that this trade-off is not necessarily expressed at the population-level and, apart from seed heteromorphic species, the individual-level. In the seed heteromorphic *Dimorphotheca*, individual fruit that are highly dormant do not possess structures for wind dispersal and vice versa, which is consistent with the idea that physiological or weight constraints may drive a trade-off. Spatial and temporal dispersal as alternative risk-reducing

strategies have important consequences for population dynamics and species persistence, emphasising the need for further studies that integrate risk-spreading trade-offs and improve our understanding of the causes, consequences and constraints on their evolution. Indeed, my overall findings suggest that dispersal in space and time may be selected for by entirely different selection pressures.

Spatial dispersion patterns and conspecific density is expected to strongly affect the fecundity of individuals in multi-species co-flowering communities. In support of this, my results underscore the importance of heterospecific interference and mate availability on fecundity. Both of these mechanisms are affected by plant density and dispersion, and operate independently of quantitative variation in pollinator visitation rates to flowers. Indeed, my findings emphasise the importance of including both pollinator observations and fecundity measures to tease apart the contributions of different pollinator-mediated interactions in communities. Community structure is also important: at low abundance and scattered dispersion patterns, individuals in my experimental arrays performed poorly in terms of fruit set. Self-compatibility, however, ensured consistent fruit set and may provide a mechanism to enhance fecundity for species with scattered distributions in a community. Such scattered distributions may be evident in species with highly dispersive propagules, which is in accord with the association between selfing and high dispersal among annual South African daisies that I established in Chapter 2.

Taken together, my research illustrates that dispersal, dormancy and seed heteromorphism may function as alternative risk-reducing strategies, enabling plants to persist in unpredictable environments. However, I show that the effects of longevity and phylogenetic relatedness are significant, and that studies focussing on covariation in dispersal and dormancy need to take into account the role of life history strategies and evolutionary relationships. My findings also highlight the importance of selfing ability as a risk-reducing strategy in biotically unfavourable or unpredictable environments. For example, selfing ability may be advantageous when mates are limited following long-distance dispersal or when individuals occur at low relative abundance in a community, or when the probability of heterospecific interference is high.

My research sheds some light on the many contradicting hypotheses that exist to predict and explain interactions among various risk-reducing strategies. However, it is also evident that the current theory literature is inadequate to explain the complexities observed in southern African daisies. On the other hand, studies of this nature are limited and do not consistently provide support for these theoretical predictions. Future research will benefit from additional empirical tests of dispersal-dormancy theoretical predictions, particularly studies which simultaneously test for the influence of local determinants (e.g. pollen and resource availability) on fruit set, which could strongly influence the strength of selection to shape allocation patterns. For example, the absence of certain predicted patterns or trade-offs at the level of populations within species could be due to an absence of selection across space, as implied in some of my research chapters. However, one of the most insightful contributions to the study of range margins over the last couple of decades has been the idea that marginal populations just might not be at their adaptive optimum because of the influx of genes via migration from the species' core populations (Kirkpatrick & Barton, 1997; see Sexton *et al.*, 2009 for review). This idea might be explored in the context of the present study's findings, and the possibility entertained that natural selection might not be as powerful to draw populations to their optimum as is sometimes presumed, and as is implied by most of the theoretical models cited in this dissertation.

Risk-reducing strategies may be especially important as environments become increasingly unpredictable due to global climate change. Understanding the effects of climate change on biodiversity poses a major challenge to biologists in the 21st century, particularly in species-rich regions where many species may face the risk of extinction due to the loss of suitable habitat, range shifts, etc. (Hannah, Midgley, & Millar, 2002; Hannah, Midgley, Lovejoy, *et al.*, 2002). The Succulent Karoo biome and the Cape Floristic Region are both counted among the world's 25 biodiversity hotspots (Myers *et al.*, 2000) – areas of remarkably high levels of endemism and species richness – but both are under imminent threat from climate change (Malcolm *et al.*, 2006; Midgley & Thuiller, 2007). Some of the predicted changes for these regions include range shifts, range contractions and increasingly unpredictable rainfall events (Midgley *et al.*, 2003; Midgley & Thuiller, 2007). Moreover, anthropogenic effects may drive habitat fragmentation which may affect pollinator diversity and consequently plant reproductive

success (Donaldson *et al.*, 2002). Understanding how organisms might respond to these threats is imperative. Yet, surprisingly little information is available on the pollination biology and dispersal of Namaqualand plants and future research will benefit greatly from a more in depth understanding of the region's unique ecology.

Increased awareness of risk-reducing strategies has important conservation implications (Eriksson, 2000; Buoro & Carlson, 2014). From this perspective, I suggest that Namaqualand daisies exhibiting the selfing dispersive syndrome (Chapter 2) may be at an advantage compared to those exhibiting the outcrossing/low dispersal syndrome. The latter may be particularly vulnerable to range shifts/contractions and changes in the pollinator environment, because they essentially exhibit “specialist” breeding system and dispersal behaviour (Bond, 1994; E Kisdi, 2002). Their only compensation may be the ability to hedge their bets in time through dormancy (Chapter 5), although I found little evidence for increased investment in dormancy in relation to increased climatic unpredictability. This research contributes to our understanding of the ecology of spatial and temporal risk-reducing strategies and the intricate relationships among these strategies that may enable plants to persist in changing environments.

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Supplementary information

Table S2.1. Localities of range-edge (E) and central (C) populations of thirteen Asteraceae species from South Africa.

| Site | Range position | GPS South | GPS East |
|---|----------------|--------------|--------------|
| <i>Dimorphotheca pluvialis</i> (L.) Moench | | | |
| Avontuur | C | 30°22' 52.0" | 17°29' 34.5" |
| Varsch | E | 31°30' 01.2" | 18°43' 01.2" |
| <i>Dimorphotheca polyptera</i> DC. | | | |
| Suurdam | E | 30°38' 09.0" | 18°25' 47.1" |
| <i>Dimorphotheca sinuata</i> DC. | | | |
| Stein Koppie | C | 29°15' 50.5" | 17°44' 59.1" |
| Moedverloor1 | E | 31°38' 00.7" | 19°14' 40.2" |
| <i>Gazania lichtensteinii</i> Less. | | | |
| Tankwa2 | C | 31°55' 38.1" | 19°48' 57.7" |
| Carminea Site | E | 31°23' 25.6" | 18°39' 18.8" |
| <i>Gazania tenuifolia</i> Less. | | | |
| Roodebergs | C | 30°32' 41.3" | 17°59' 27.6" |
| Stein Ridge | C | 29°11' 02.7" | 17°49' 23.6" |
| Kliprand2 | E | 30°29' 03.4" | 18°39' 52.2" |
| Suurdam | E | 30°38' 09.0" | 18°25' 47.1" |
| <i>Osteospermum amplexans</i> (Harv.) T. Norl. | | | |
| Kamies | C | 30°12' 20.5" | 17°56' 13.5" |
| Naresie | E | 31°18' 36.9" | 19°29' 20.8" |
| <i>Osteospermum hyoseroides</i> (DC.) T. Norl. | | | |
| Kamies | C | 30°12' 20.5" | 17°56' 13.5" |
| Klipfontein | E | 30°29' 58.5" | 17°56' 02.6" |
| <i>Osteospermum microcarpum</i> (Harv.) T. Norl. var. <i>microcarpum</i> | | | |
| Carminea Site | E | 31°25' 40.1" | 18°38' 19.4" |
| <i>Osteospermum monstrosum</i> (Burm.f.) J.C. Manning & Goldblatt | | | |
| Garies-Bitter | C | 30°52' 06.3" | 18°09' 17.6" |
| Kners-Eskom | C | 31°34' 54.8" | 18°29' 51.1" |
| Calvinia | E | 31°30' 42.1" | 19°44' 13.2" |
| <i>Ursinia anthemoides</i> (L.) Poir. | | | |
| VanClan3 | C | 31°59' 16.8" | 18°45' 29.6" |
| Moedverloor1 | E | 31°38' 00.7" | 19°14' 40.2" |
| <i>Ursinia cakilefolia</i> DC. | | | |
| Skilpad | C | 30°09' 48.8" | 17°48' 04.5" |
| Moedverloor2 | E | 31°36' 44.8" | 19°14' 13.2" |
| Nieuw Ingang | E | 31°22' 17.6" | 19°06' 33.4" |
| <i>Ursinia calenduliflora</i> (DC.) N.E.Br. | | | |
| Bovlei | C | 30°14' 34.8" | 18°03' 11.4" |
| <i>Ursinia nana</i> DC. | | | |
| Stein Koppie | C | 29°15' 50.5" | 17°44' 59.1" |
| GariesB | E | 30°32' 43.0" | 17°57' 34.8" |

Table S2.2. Indices of self-incompatibility (ISI) and autofertility relative to hand cross-pollination (AF_x) as well as the mean fall time (\pm SE) for central (C) and range-edge (E) populations of thirteen annual Asteraceae species from South Africa.

| Species | Population | Range position | ISI | AF_x | Fall time |
|----------------------------|---------------|----------------|-------|--------|-----------------|
| <i>D. pluvialis</i> | Avontuur | C | 0.93 | 0.04 | 1.45 \pm 0.02 |
| | Varsch | E | 0.75 | 1.15 | 1.40 \pm 0.03 |
| <i>D. polyptera</i> | Suurdam | M | 0.92 | 0.05 | 1.86 \pm 0.05 |
| <i>D. sinuata</i> | Stein Koppie | C | 0.81 | 0.13 | 1.98 \pm 0.04 |
| | Moedverloor1 | E | 0.90 | 0.07 | 1.81 \pm 0.46 |
| <i>G. lichtensteinii</i> | Tankwa2 | C | 0.83 | 0.05 | 2.82 \pm 0.03 |
| | Carminea Site | E | 0.99 | 0.06 | 2.68 \pm 0.04 |
| <i>G. tenuifolia</i> | Roodebergs | C | -0.04 | 1.05 | 2.65 \pm 0.04 |
| | Stein Ridge | C | -0.16 | 1.05 | 2.87 \pm 0.03 |
| | Kliprand2 | E | -0.20 | 0.92 | 2.86 \pm 0.05 |
| | Suurdam | E | 0.00 | 1.03 | 2.38 \pm 0.04 |
| <i>O. amplexens</i> | Kamies | C | 0.78 | 0.05 | 1.30 \pm 0.02 |
| | Naresie | E | 0.49 | 0.17 | 1.41 \pm 0.02 |
| <i>O. hyoseroides</i> | Kamies | C | 0.52 | 0.21 | 1.77 \pm 0.02 |
| | Klipfontein | E | 0.84 | 0.00 | 1.64 \pm 0.02 |
| <i>O. microcarpum</i> | Carminea Site | E | 0.82 | 0.02 | 1.26 \pm 0.02 |
| <i>O. monstrosum</i> | Garies-Bitter | C | -0.24 | 1.01 | 1.62 \pm 0.02 |
| | Calvinia | E | 0.09 | 1.04 | 1.55 \pm 0.02 |
| <i>U. anthemoides</i> | VanClan3 | C | 0.15 | 0.91 | 2.98 \pm 0.07 |
| | Moedverloor1 | E | -0.10 | 1.21 | 3.53 \pm 0.05 |
| <i>U. cakilefolia</i> | Skilpad | C | 0.95 | 0.03 | 2.23 \pm 0.04 |
| | Moedverloor2 | E | 0.99 | 0.06 | 2.56 \pm 0.04 |
| | Nieuw Ingang | E | 0.94 | 0.00 | 2.07 \pm 0.03 |
| <i>U. calenduliflora</i> * | Bovlei | C | 0.93 | 0.00 | |
| | U.cal disp. | C | | | 2.51 \pm 0.03 |
| <i>U. nana</i> | Stein Koppie | C | 0.06 | 0.83 | 2.76 \pm 0.04 |
| | GariesB | E | -0.25 | 0.97 | 2.73 \pm 0.03 |

* For *Ursinia calenduliflora* we measured breeding system traits at Bovlei but used the mean fall time calculated across four nearby populations that were also in the range centre.

Table S2.3. Analysis of deviance for the effect of range position and pollination treatment in fruit set in ten annual Asteraceae species from South Africa.

| Species | Φ | Effect | Change in deviance | Quasi-F value | df ₁ | df ₂ | p value |
|--------------------------|--------|-----------------------|--------------------|---------------|-----------------|-----------------|---------|
| <i>D. pluvialis</i> | 3.45 | Pollination treatment | 481.89 | 72.57 | 2 | 82 | <0.001 |
| | | Range position | 0.03 | 0.01 | 1 | 82 | 0.927 |
| | | P*R | 24.1 | 3.88 | 2 | 80 | 0.0246 |
| <i>D. polyptera</i> | 2.72 | Pollination treatment | 460.64 | 98.68 | 2 | 45 | < 0.001 |
| <i>D. sinuata</i> | 5.06 | Pollination treatment | 722.9 | 77.49 | 2 | 85 | < 0.001 |
| | | Range position | 106.18 | 22.78 | 1 | 85 | < 0.001 |
| | | P*R | 9.2 | 0.99 | 2 | 83 | 0.377 |
| <i>G. lichtensteinii</i> | 3.48 | Pollination treatment | 397.04 | 49.65 | 2 | 51 | <0.001 |
| | | Range position | 0.00 | 0.00 | 1 | 51 | 1.00 |
| | | P*R | 15.39 | 2.00 | 2 | 49 | 0.146 |
| <i>G. tenuifolia</i> | 1.22 | Pollination treatment | 1.15 | 0.46 | 2 | 126 | 0.634 |
| | | Range position | 0.31 | 0.25 | 1 | 126 | 0.621 |
| | | P*R | 0.03 | 0.015 | 2 | 124 | 0.985 |
| <i>O. amplexens</i> | 4.21 | Pollination treatment | 267.75 | 33.26 | 2 | 79 | < 0.001 |
| | | Range position | 0.02 | 0.01 | 1 | 79 | 0.941 |
| | | P*R | 18.9 | 2.43 | 2 | 77 | 0.095 |
| <i>O. hyoseroides</i> | 4.07 | Pollination treatment | 114.32 | 14.62 | 2 | 58 | <0.001 |
| | | Range position | 62.72 | 16.04 | 1 | 58 | <0.001 |
| | | P*R | 11.49 | 1.49 | 2 | 56 | 0.233 |
| <i>O. microcarpum</i> | 3.97 | Pollination treatment | 63.71 | 6.32 | 2 | 9 | 0.019 |
| <i>O. monstrosum</i> | 1.77 | Pollination treatment | 0.98 | 0.24 | 2 | 66 | 0.789 |
| | | Range position | 7.15 | 3.46 | 1 | 66 | 0.067 |
| | | P*R | 2.47 | 0.59 | 2 | 64 | 0.558 |
| <i>U. anthemoides</i> | 3.82 | Pollination treatment | 0.93 | 0.13 | 2 | 65 | 0.881 |
| | | Range position | 3.08 | 0.84 | 1 | 65 | 0.364 |
| | | P*R | 3.29 | 0.44 | 2 | 63 | 0.647 |
| <i>U. cakilefolia</i> | 5.99 | Pollination treatment | 2749.62 | 270.84 | 2 | 122 | < 0.001 |
| | | Range position | 20.12 | 3.97 | 1 | 122 | 0.049 |
| | | P*R | 1.95 | 0.19 | 2 | 120 | 0.828 |
| <i>U. calenduliflora</i> | 4.22 | Pollination treatment | 541.66 | 75.6 | 2 | 52 | < 0.001 |
| <i>U. nana</i> | 3.30 | Pollination treatment | 8.36 | 1.20 | 2 | 75 | 0.306 |
| | | Range position | 31.93 | 9.18 | 1 | 75 | 0.003 |
| | | P*R | 4.43 | 0.63 | 2 | 73 | 0.536 |

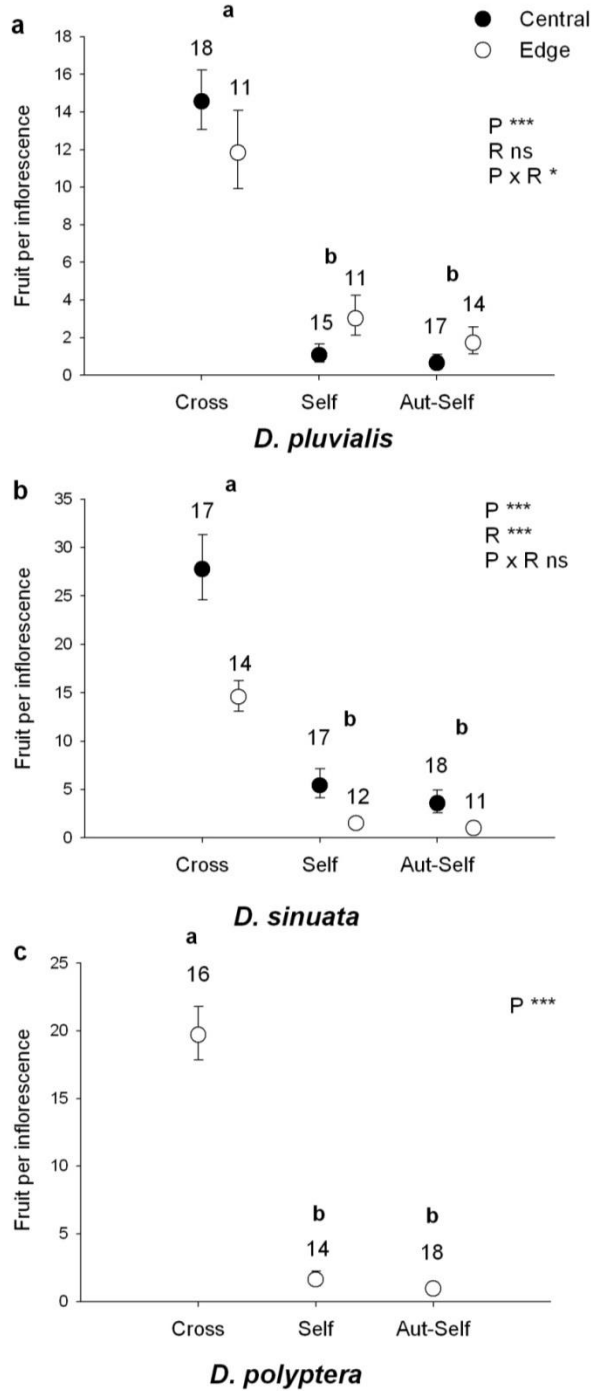
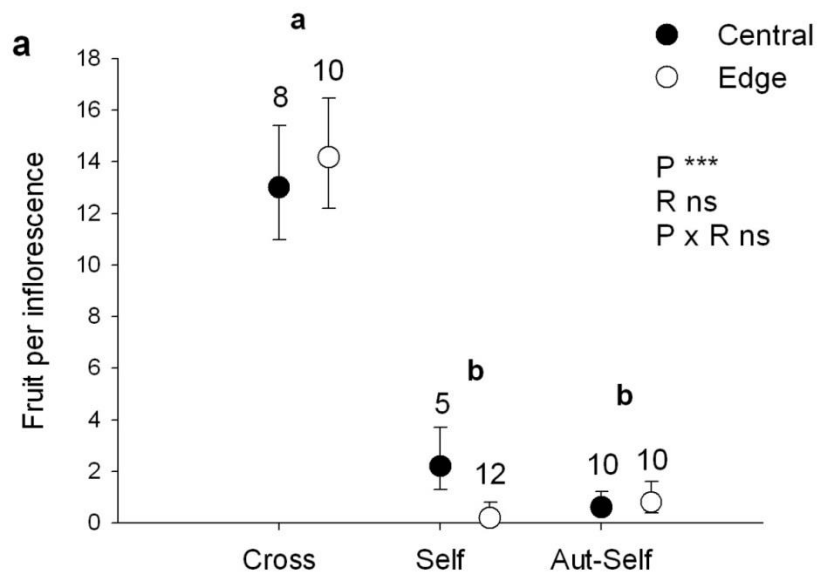
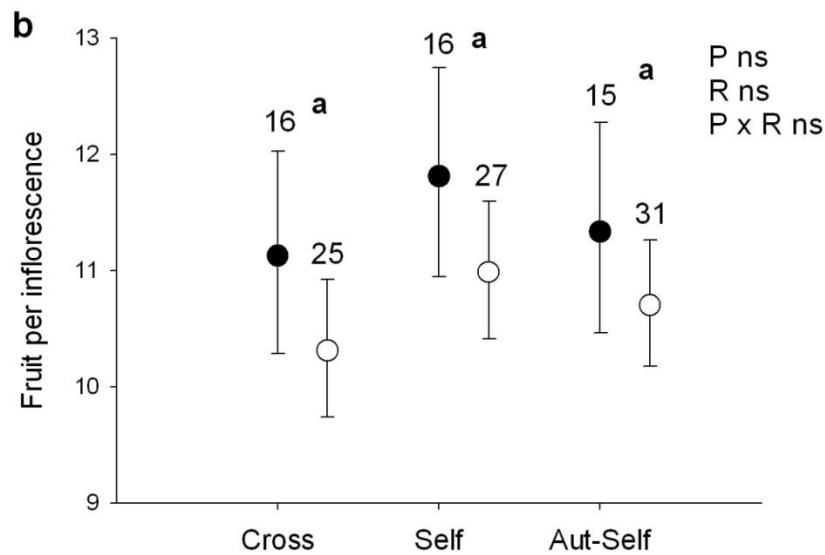


Fig. S2.1. Mean \pm SE fruit set for controlled pollination experiments on *Dimorphotheca pluvialis* (a), *D. sinuata* (b) and *D. polyptera* (c). Means \pm SE estimated for each population separately from GLMs and back-transformed from the scale of the linear predictor. P = Pollination treatment, R = Range position, ns = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Pollination treatments marked with different letters differ significantly.



G. lichtensteinii



G. tenuifolia

Fig. S2.2. Mean \pm SE fruit set for controlled pollination experiments on *Gazania lichtensteinii* (a) and *G. tenuifolia*. Means \pm SE estimated for each population separately from GLMs and back-transformed from the scale of the linear predictor. P = Pollination treatment, R = Range position, ns = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Pollination treatments marked with different letters differ significantly.

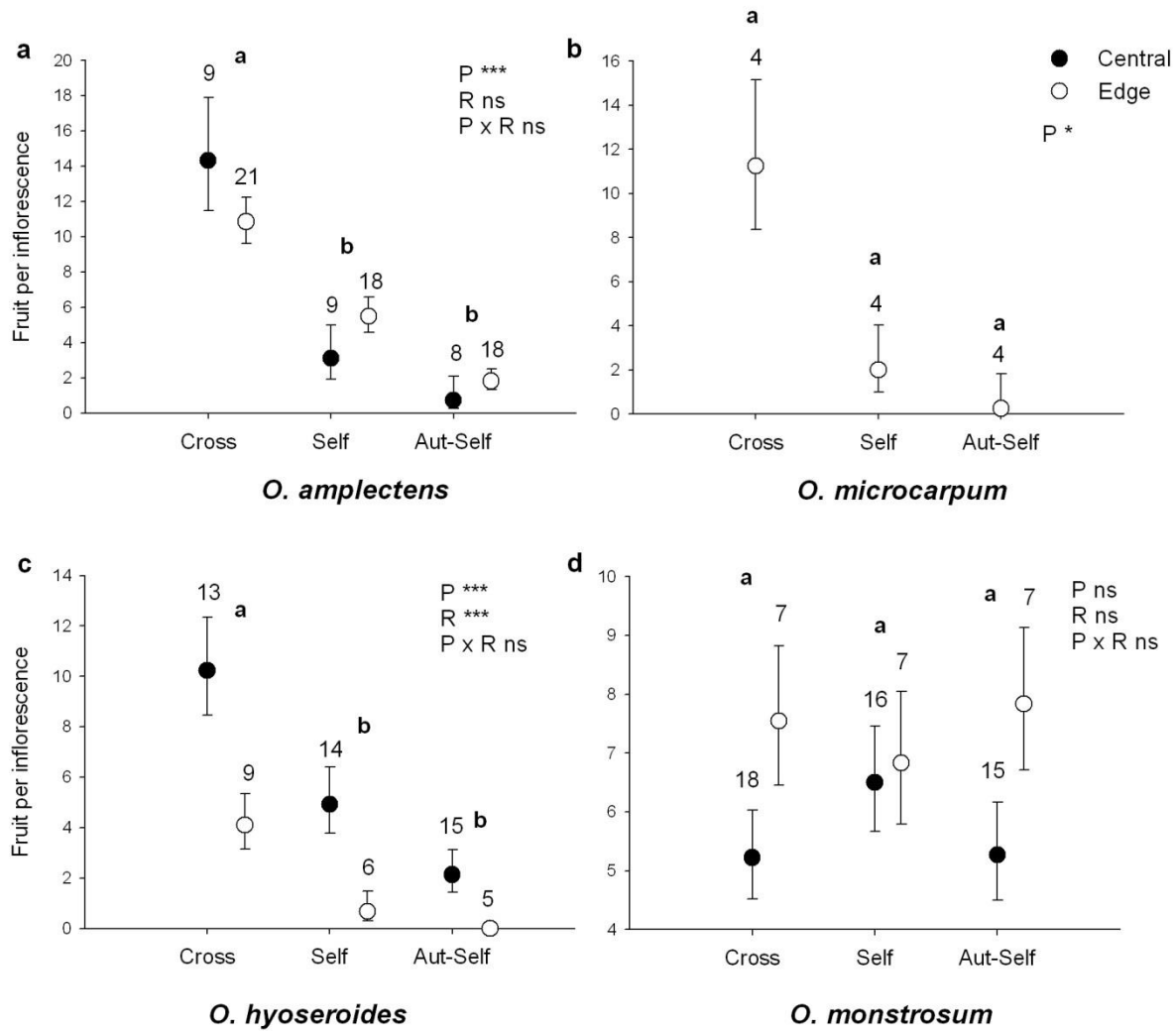


Fig. S2.3. Mean \pm SE fruit set for controlled pollination experiments on *Osteospermum amplexens* (a), *O. microcarpum* (b), *O. hyoseroides* (c) and *O. monstrosum* (d). Means \pm SE estimated for each population separately from GLMs and back-transformed from the scale of the linear predictor. P = Pollination treatment, R = Range position, ns = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Pollination treatments marked with different letters differ significantly.

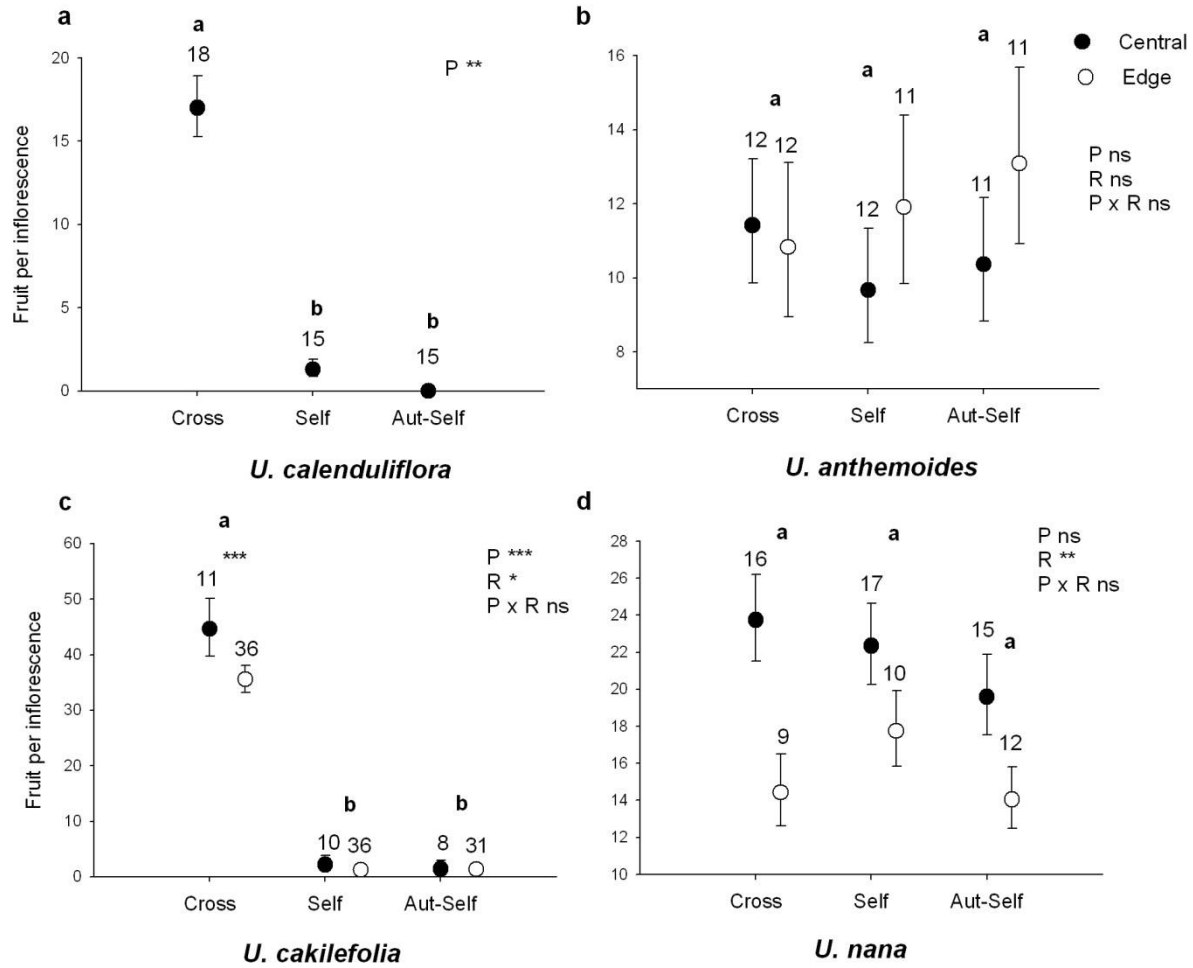


Fig. S2.4. Mean \pm SE fruit set for controlled pollination experiments on *Ursinia calenduliflora* (a), *U. anthemoides* (b), *U. cakilefolia* (c) and *U. nana* (d). Means \pm SE estimated for each population separately from GLMs and back-transformed from the scale of the linear predictor. P = Pollination treatment, R = Range position, ns = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Pollination treatments marked with different letters differ significantly.

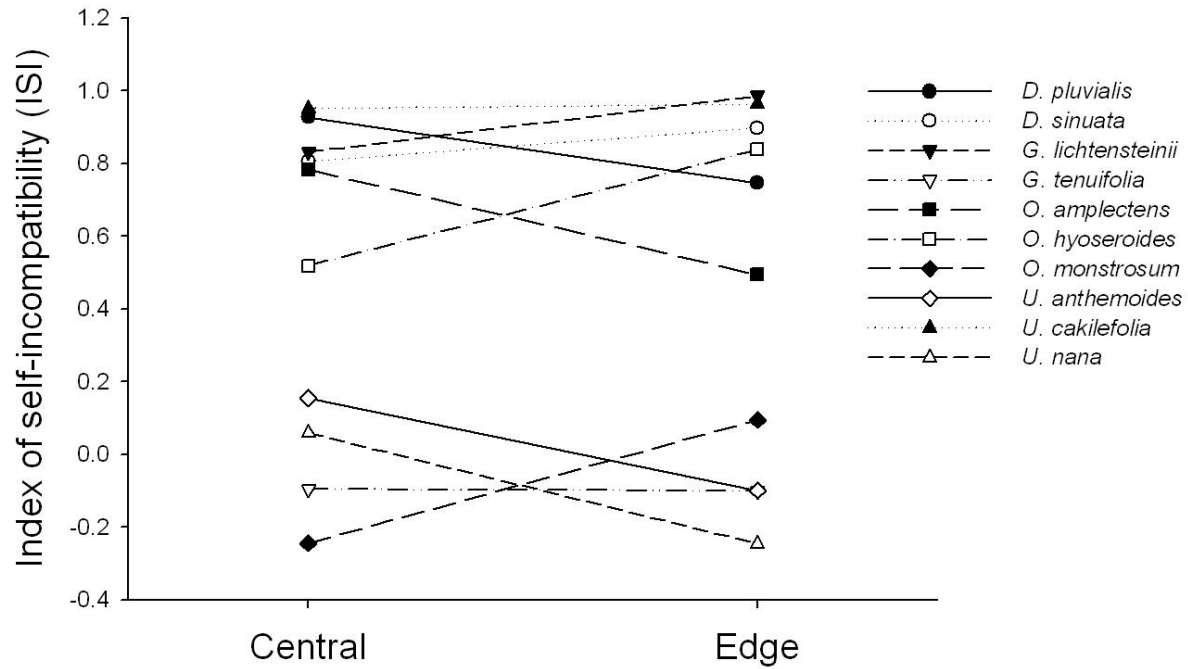


Fig. S2.5. Index of self-incompatibility (ISI) for range-edge and central populations of ten annual Asteraceae species. Across all species, range-edge populations did not differ significantly from central populations in ISI (Wilcoxon Signed Ranks tests: $V = 21$, $p = 0.557$).

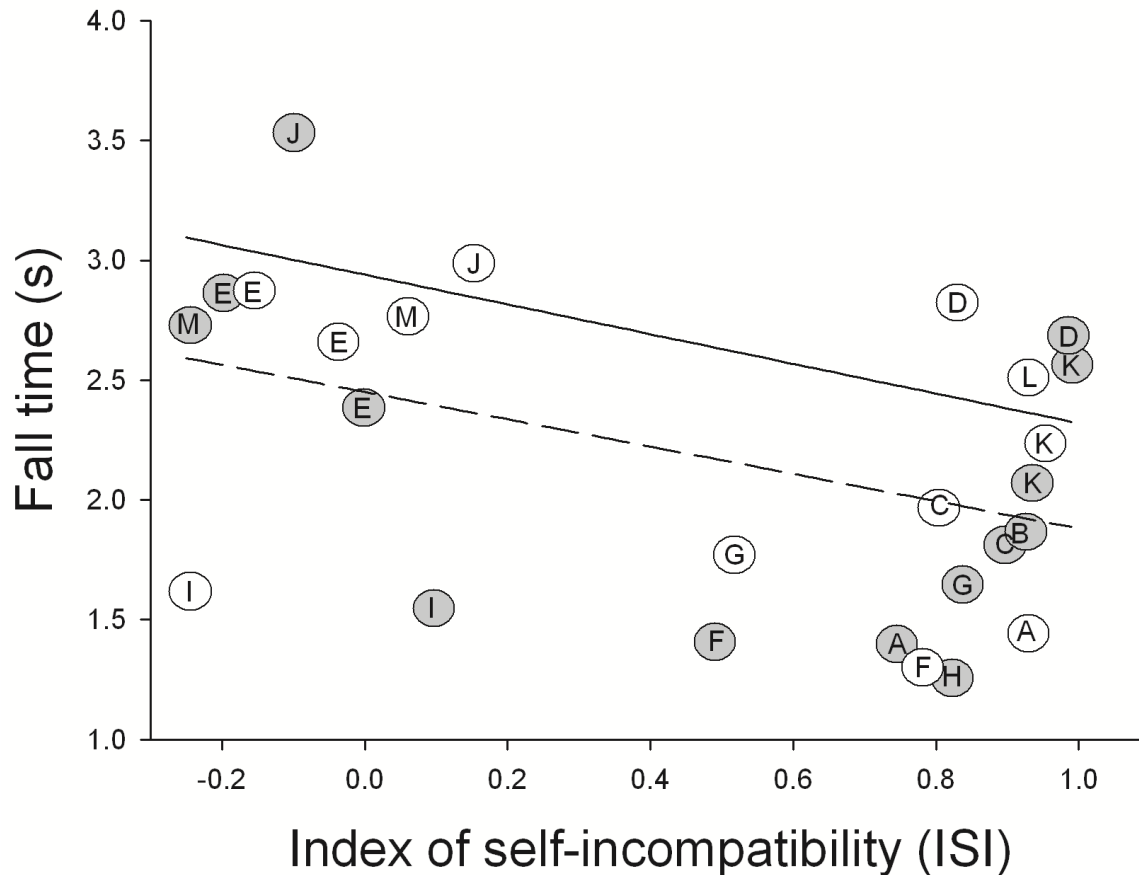


Fig S2.6. The association between fall time, a measure of dispersal ability, and index of self-incompatibility (ISI) for populations of thirteen annual Asteraceae species. ISI was negatively associated with fall time, taking phylogeny into account ($\beta = -0.62$, $t_{24} = 3.21$, $p = 0.003$). The model including the hypothesised phylogeny (solid line; see text) was superior to the model with all phylogenetic relationships unresolved (dashed line; equivalent to ordinary least squares regression, $\Delta\text{AIC} \gg 10$). Nevertheless, the relationship between ISI and fall time was also significant in this analysis ($\beta = -0.57$, $t_{24} = 2.49$, $p = 0.030$). Clear circles indicate central populations and grey circles indicate range-edge populations. A = *Dimorphotheca pluvialis*, B = *D. polyptera*, C = *D. sinuata*, D = *Gazania lichtensteinii*, E = *G. tenuifolia*, F = *Osteospermum amplexans*, G = *O. hyoseroides*, H = *O. microcarpum*, I = *O. monstrosum*, J = *Ursinia anthemoides*, K = *U. cakilefolia*, L = *U. calenduliflora*, M = *U. nana*.

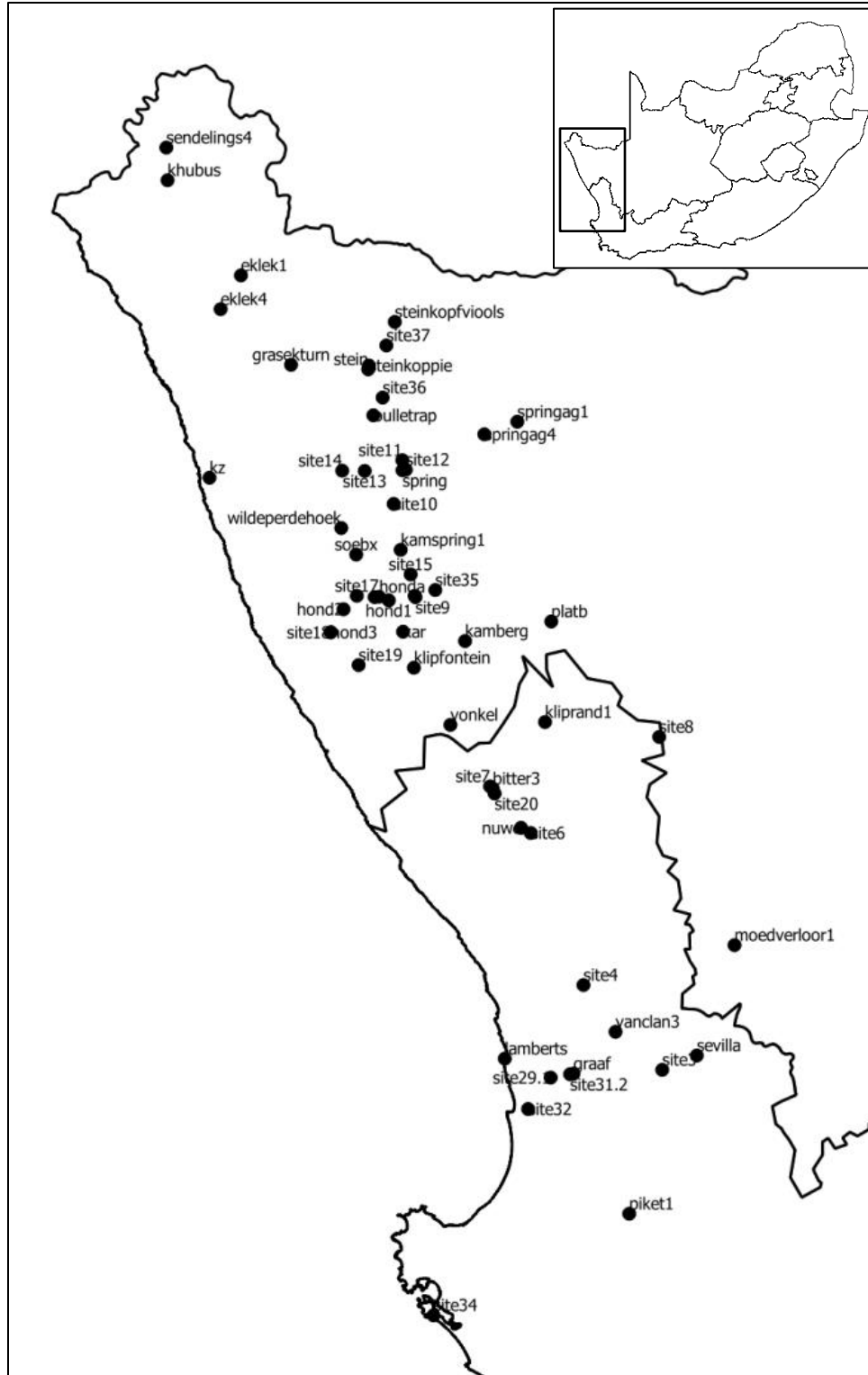


Fig. S4.1. Localities of populations of *Dimorphotheca sinuata* sampled for fruit and/or floret numbers.

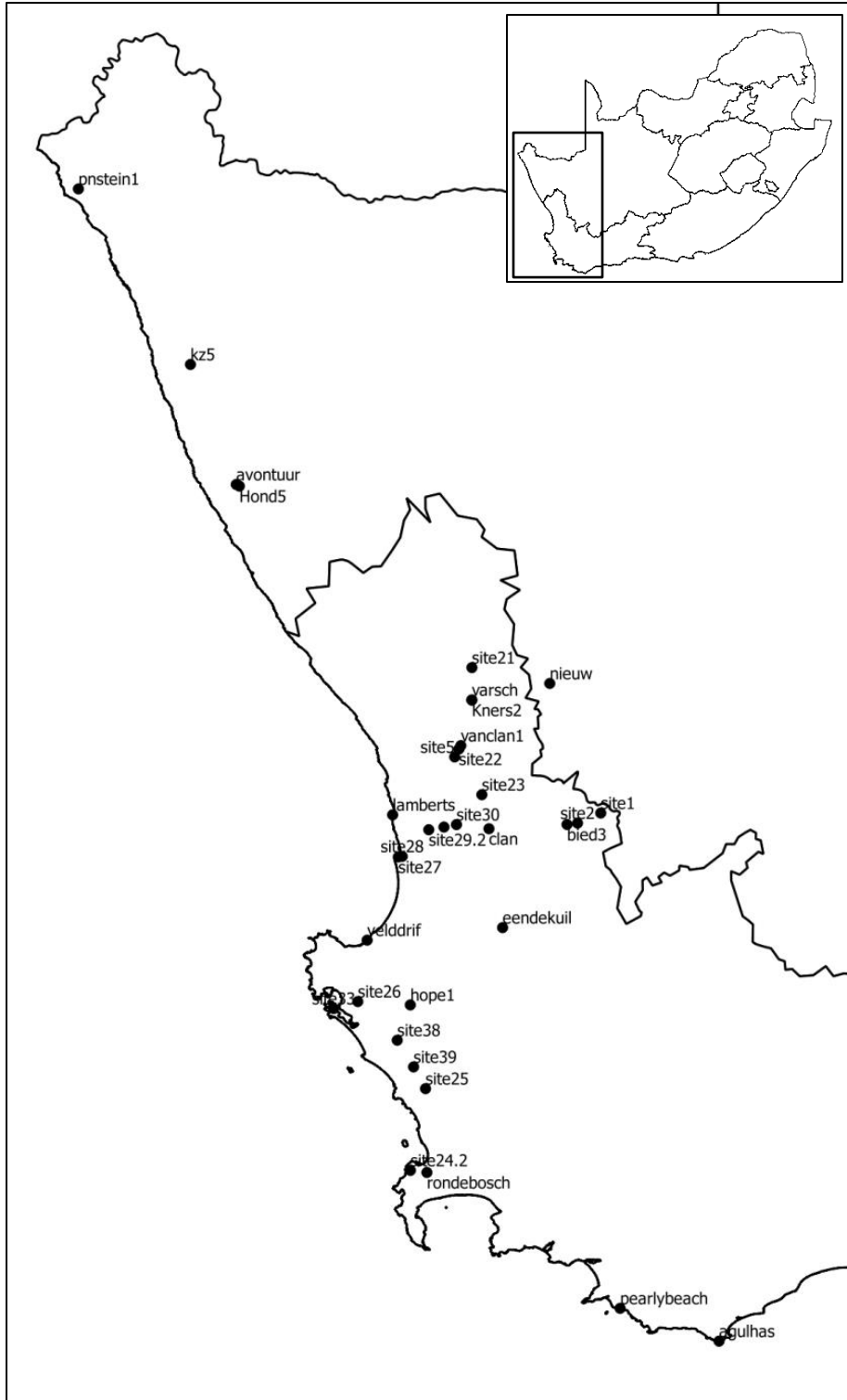


Fig. S4.2. Localities of populations of *Dimorphotheca pluvialis* sampled for fruit and/or floret numbers.



Fig. S4.3. Correlation matrix of associations between seven climatic variables: mean winter precipitation (wp), coefficient of variation of winter precipitation (cvwp), coefficient of variation of winter months (cvwm), April – June mean precipitation (ajp), April – June coefficient of variation of precipitation, July – September mean precipitation (jsp), July – September coefficient of variation of precipitation. Numbers represent correlation coefficients, colours represent the slope of the association (blue = positive, red = negative) and the shapes illustrate the shape of the scatterplot. All correlations are significant at $\alpha = 0.05$.

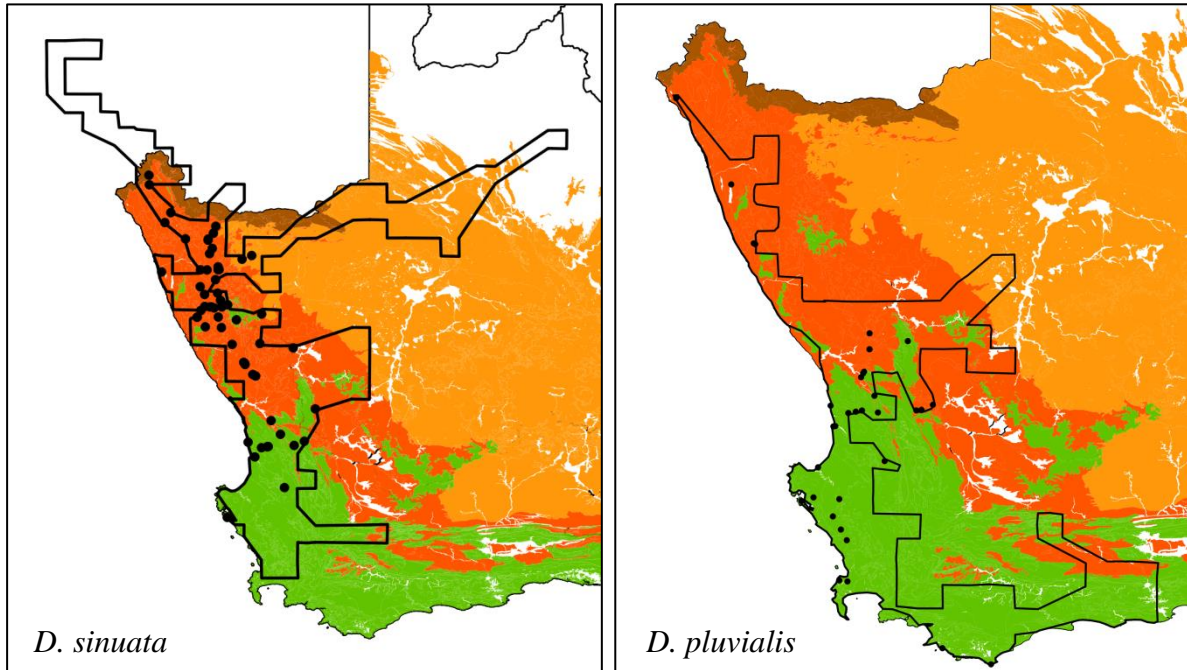


Fig. S4.4. Fine scale distribution range (black line) and populations sampled for fruit and/or floret traits (black circles) of *Dimorphotheca sinuata* (left) and *D. pluvialis* (right). The distribution range was determined by combining our own observation records obtained by extensive field work and data records in the form of quarter degree grid squares from the SIBIS database (sibis.sanbi.org; see text for details). South African vegetation biomes are indicated as: dark brown = Desert Biome, dark orange = Succulent Karoo biome, light orange = Nama Karoo biome, green = Fynbos biome (South African National Biodiversity Institute, 2006).

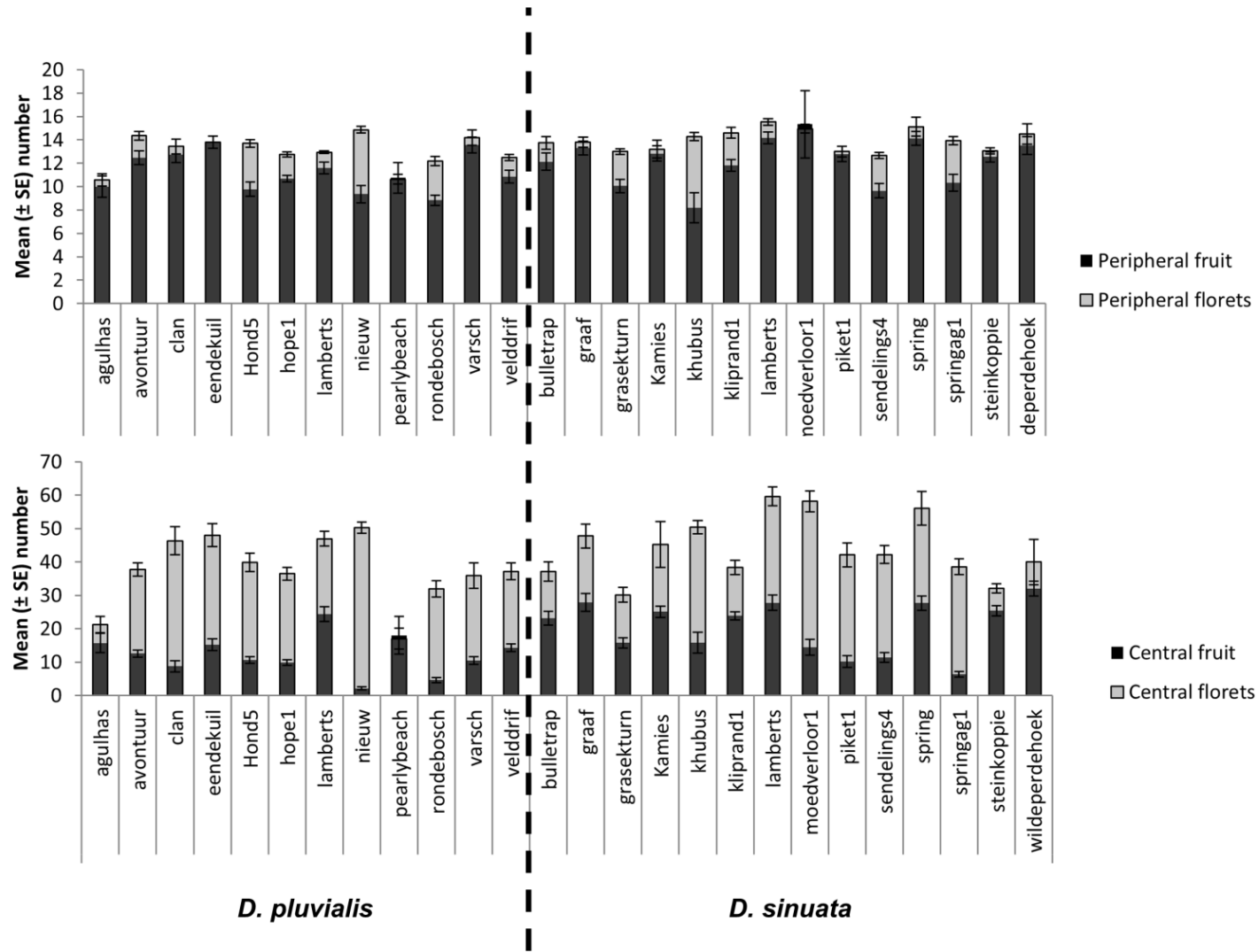


Fig. S4.5. Mean (\pm SE) number of peripheral (top) and central (bottom) fruit (black) and florets (grey) in populations of *Dimorphotheca pluvialis* and *D. sinuata*. Peripheral fruit represent the dormant, non-dispersive morph whereas central fruit are adapted for wind dispersal and germinate readily.

Table S4.1. Localities, sample sizes, mean winter precipitation, coefficient of variation (CV) of winter precipitation, mean number of central fruit, mean proportion peripheral fruit and mean numbers of central and peripheral florets sampled for 59 populations of *Dimorphotheca sinuata* and 34 populations of *D. pluvialis*. Localities, sample sizes and fruit and floret numbers are also reported for *D. polyptera* (four populations), *D. tragus* (five populations) and *D. cuneata* (one population). Climatic variables were obtained from the closest weather station(s) (data provided by the South African Weather Bureau).

| Species | Population | GPS coordinates | Altitude (m) | Number of individuals sampled for fruit counts | Number of individuals sampled for floret counts | Mean winter precipitation (mm) | CV of winter precipitation | Mean number of central fruit (\pm SE) | Mean proportion peripheral fruit (\pm SE) | Mean number of disk florets (\pm SE) | Mean number of ray florets (\pm SE) |
|-------------------|-------------|------------------------------------|--------------|--|---|--------------------------------|----------------------------|--|--|---|--|
| <i>D. sinuata</i> | Bitter3 | 30° 59' 38.0" S 18° 15' 22.5" E | 380 | 19 | | 115.59 | 0.39 | 11.61 \pm 1.31 | 0.52 \pm 0.03 | | |
| | Bulletrap | 29° 28' 04.3" S 17° 46' 05.0" E | 729 | 18 | 15 | 166.40 | 0.34 | 23.12 \pm 2.03 | 0.35 \pm 0.02 | 37.13 \pm 2.85 | 13.73 \pm 0.55 |
| | EkLek1 | 28° 53' 45.5" S 17° 13' 37.3" E | 787 | 15 | | 60.04 | 0.55 | 20.77 \pm 2.28 | 0.40 \pm 0.04 | | |
| | EkLek4 | 29° 02' 02.1" S 17° 08' 38.1" E | 359 | 22 | | 60.04 | 0.55 | 9.68 \pm 1.53 | 0.58 \pm 0.04 | | |
| | Graafwater | 32° 09' 32.5" S 18° 35' 10.7" E | 167 | 18 | 20 | 208.86 | 0.31 | 27.90 \pm 2.68 | 0.35 \pm 0.03 | 47.75 \pm 3.60 | 13.80 \pm 0.43 |
| | Grasekturm | 29° 15' 41.0" S 17° 25' 54.3" E | 395 | 20 | 11 | 108.83 | 0.53 | 15.80 \pm 1.51 | 0.40 \pm 0.02 | 30.18 \pm 2.17 | 13.00 \pm 0.23 |
| | Hond1 | 30° 13' 27.2" S 17° 49' 53.1" E | 689 | 12 | | 182.53 | 0.41 | 12.81 \pm 2.07 | 0.46 \pm 0.04 | | |
| | Hond2 | 30° 15' 38.2" S 17° 38' 47.0" E | 258 | 24 | | 221.74 | 0.42 | 19.26 \pm 2.02 | 0.41 \pm 0.02 | | |
| | Hond3 | 30° 21' 16.3" S 17° 35' 38.3" E | 252 | 20 | | 186.16 | 0.40 | 21.48 \pm 1.99 | 0.38 \pm 0.02 | | |
| | HondA | 30° 12' 34.2" S 17° 47' 30.3" E | 655 | 19 | | 182.53 | 0.41 | 35.04 \pm 2.48 | 0.30 \pm 0.01 | | |
| | Kamberg | 30° 23' 26.1" S 18° 08' 35.2" E | 1115 | 11 | | 323.24 | 0.56 | 32.12 \pm 4.37 | 0.37 \pm 0.02 | | |
| | Kamieskroon | 30° 12' 20.5" S 17° 56' 13.5" E | 755 | 20 | 20 | 182.53 | 0.41 | 25.10 \pm 1.67 | 0.35 \pm 0.02 | 45.20 \pm 6.86 | 13.20 \pm 0.76 |
| | Kamspring1 | 30° 01' 04.0" S 17° 52' 47.8" E | 564 | 3 | | 130.09 | 0.44 | 8.28 \pm 1.41 | 0.45 \pm 0.09 | | |
| | Karkams | 30° 21' 08.4" S 17° 53' 22.8" E | 749 | 22 | | 260.94 | 0.44 | 9.48 \pm 1.21 | 0.54 \pm 0.03 | | |
| | Khubus | 28° 30' 25.2" S 16° 55' 36.9" E | 399 | 5 | 17 | 67.68 | 0.51 | 15.80 \pm 3.09 | 0.36 \pm 0.09 | 50.41 \pm 1.93 | 14.29 \pm 0.35 |
| | Klipfontein | 30° 29' 58.5" S 17° 56' 02.6" E | 504 | 10 | | 210.9 | 0.21 | 24.42 \pm 2.68 | 0.34 \pm 0.03 | | |
| | Kliprand1 | 30° 43' 18.0" S 18° 28' 11.7" E | 514 | 20 | 20 | 105.25 | 0.33 | 23.87 \pm 1.18 | 0.33 \pm 0.01 | 38.40 \pm 2.14 | 14.60 \pm 0.46 |
| | Kleinzee | 29° 43' 22.4" S 17° 05' 54.3" E | 116 | 12 | | 69.08 | 0.49 | 27.55 \pm 2.65 | 0.35 \pm 0.02 | | |

| | | | | | | | | | | |
|--------------|------------------------------------|------|----|----|--------|------|--------------|-------------|--------------|--------------|
| Lamberts | 32° 05' 51.5" S 18° 18' 19.6" E | 18 | 19 | 40 | 123.25 | 0.41 | 27.82 ± 2.22 | 0.35 ± 0.02 | 59.63 ± 2.86 | 15.53 ± 0.27 |
| Moedverloor1 | 31° 38' 00.7" S 19° 14' 40.2" E | 671 | 15 | 20 | 219.47 | 0.33 | 14.47 ± 2.33 | 0.50 ± 0.06 | 58.15 ± 3.15 | 14.95 ± 0.37 |
| Nuwerus | 31° 09' 14.3" S 18° 22' 18.6" E | 346 | 7 | | 123.34 | 0.37 | 20.10 ± 4.10 | 0.49 ± 0.09 | | |
| Piket1 | 32° 43' 53.9" S 18° 48' 50.6" E | 138 | 12 | 20 | 243.76 | 0.30 | 10.22 ± 1.76 | 0.59 ± 0.04 | 42.15 ± 3.58 | 13.00 ± 0.45 |
| Platbakkies | 30° 19' 00.1" S 18° 26' 09.9" E | 1058 | 12 | | 166.73 | 0.45 | 20.75 ± 3.76 | 0.49 ± 0.05 | | |
| Sendelings4 | 28° 22' 24.6" S 16° 55' 18.8" E | 246 | 21 | 18 | 78.85 | 0.57 | 11.42 ± 1.44 | 0.50 ± 0.03 | 42.22 ± 2.66 | 12.67 ± 0.27 |
| Sevilla | 32° 05' 04.9" S 19° 05' 26.0" E | 323 | 10 | | 199.48 | 0.38 | 25.62 ± 4.62 | 0.34 ± 0.02 | | |
| Site10 | 29° 49' 48.1" S 17° 51' 04.6" E | 751 | 20 | | 168.26 | 0.34 | 33.25 ± 3.17 | 0.37 ± 0.04 | | |
| Site11 | 29° 39' 05.0" S 17° 53' 12.7" E | - | 20 | | 168.26 | 0.34 | 24.55 ± 2.44 | 0.42 ± 0.03 | | |
| Site12 | 29° 41' 25.0" S 17° 54' 02.5" E | 831 | 20 | | 168.26 | 0.34 | 16.80 ± 3.50 | 0.58 ± 0.05 | | |
| Site13 | 29° 41' 42.7" S 17° 43' 58.7" E | 551 | 20 | | 150.82 | 0.34 | 9.15 ± 2.08 | 0.68 ± 0.05 | | |
| Site14 | 29° 41' 38.9" S 17° 38' 26.9" E | 591 | 19 | | 133.38 | 0.34 | 8.89 ± 2.19 | 0.63 ± 0.05 | | |
| Site15 | 30° 07' 05.7" S 17° 55' 14.3" E | 766 | 20 | | 182.53 | 0.41 | 9.25 ± 1.85 | 0.63 ± 0.04 | | |
| Site16 | 30° 12' 39.2" S 17° 46' 24.4" E | 686 | 20 | | 182.53 | 0.41 | 23.85 ± 2.65 | 0.40 ± 0.03 | | |
| Site17 | 30° 12' 20.3" S 17° 42' 02.6" E | 359 | 20 | | 132.84 | 0.34 | 17.20 ± 3.07 | 0.47 ± 0.05 | | |
| Site18 | 30° 21' 17.5" S 17° 35' 38.0" E | 240 | 20 | | 168.24 | 0.44 | 24.80 ± 3.14 | 0.40 ± 0.04 | | |
| Site19 | 30° 29' 19.6" S 17° 42' 29.1" E | 217 | 20 | | 210.9 | 0.21 | 14.45 ± 2.04 | 0.51 ± 0.04 | | |
| Site20 | 31° 00' 49.7" S 18° 15' 49.7" E | 384 | 20 | | 123.34 | 0.37 | 19.90 ± 2.19 | 0.43 ± 0.03 | | |
| Site29.1 | 32° 10' 30.4" S 18° 29' 31.1" E | 128 | 20 | | 208.86 | 0.31 | 20.30 ± 2.72 | 0.48 ± 0.05 | | |
| Site3 | 32° 08' 36.3" S 18° 56' 56.2" E | 586 | 20 | | 166.40 | 0.34 | 2.80 ± 0.69 | 0.78 ± 0.06 | | |
| Site31.2 | 32° 09' 40.3" S 18° 34' 20.2" E | 150 | 20 | | 208.86 | 0.31 | 16.85 ± 2.16 | 0.46 ± 0.04 | | |
| Site32 | 32° 18' 12.8" S 18° 24' 02.5" E | 133 | 20 | | 182.14 | 0.37 | 14.80 ± 2.93 | 0.56 ± 0.06 | | |
| Site34 | 33° 08' 48.7" S 18° 00' 50.8" E | 48 | 20 | | 239.75 | 0.41 | 4.70 ± 1.06 | 0.76 ± 0.04 | | |
| Site35 | 30° 10' 55.1" S 18° 01' 16.9" E | 1038 | 20 | | 208.24 | 0.44 | 4.75 ± 1.03 | 0.75 ± 0.04 | | |

| | | | | | | | | | | |
|----------------------|------------------------------------|------|----|----|--------|--------|--------------|-------------|--------------|--------------|
| Site36 | 29° 23' 43.4" S 17° 48' 22.1" E | 896 | 20 | | 108.83 | 0.53 | 16.35 ± 2.75 | 0.47 ± 0.04 | | |
| Site37 | 29° 10' 56.8" S 17° 49' 17.0" E | 949 | 17 | | 108.83 | 0.53 | 6.53 ± 1.38 | 0.61 ± 0.05 | | |
| Site4 | 31° 47' 48.7" S 18° 37' 37.3" E | 85 | 20 | | 289.67 | 0.33 | 6.55 ± 1.17 | 0.70 ± 0.05 | | |
| Site6 | 31° 10' 30.5" S 18° 24' 41.4" E | 344 | 20 | | 123.34 | 0.37 | 13.40 ± 2.69 | 0.44 ± 0.05 | | |
| Site7 | 30° 59' 04.3" S 18° 14' 43.1" E | 379 | 20 | | 115.59 | 0.39 | 27.80 ± 2.57 | 0.37 ± 0.03 | | |
| Site8 | 30° 46' 56.9" S 18° 56' 11.6" E | 289 | 20 | | 105.25 | 182.53 | 12.20 ± 2.18 | 0.53 ± 0.05 | | |
| Site9 | 30° 12' 40.3" S 17° 56' 25.0" E | 768 | 20 | | 182.53 | 0.41 | 30.10 ± 4.32 | 0.37 ± 0.03 | | |
| SoebX | 30° 02' 13.6" S 17° 41' 53.1" E | 650 | 10 | | 182.53 | 0.41 | 30.57 ± 2.56 | 0.33 ± 0.02 | | |
| Springbok | 29° 41' 33.4" S 17° 53' 14.7" E | 856 | 20 | 16 | 168.26 | 0.34 | 27.69 ± 2.19 | 0.35 ± 0.01 | 56.06 ± 5.06 | 15.13 ± 0.83 |
| SpringAg1 | 29° 29' 38.4" S 18° 21' 23.9" E | 970 | 11 | 14 | 126.21 | 0.41 | 6.33 ± 0.81 | 0.63 ± 0.04 | 38.54 ± 2.37 | 13.93 ± 0.34 |
| SpringAg4 | 29° 32' 43.6" S 18° 13' 18.6" E | 1017 | 9 | | 126.21 | 0.41 | 17.89 ± 2.00 | 0.42 ± 0.04 | | |
| Steinkopf | 29° 16' 47.2" S 17° 44' 49.7" E | 838 | | 18 | 108.83 | 0.53 | | | 38.78 ± 2.12 | 14.89 ± 0.42 |
| Steinkopf-Viools | 29° 05' 09.9" S 17° 51' 21.1" E | 809 | 9 | | 108.83 | 0.53 | 11.61 ± 1.94 | 0.48 ± 0.06 | | |
| Steinkoppie | 29° 15' 50.5" S 17° 44' 59.1" E | 823 | 20 | 20 | 108.83 | 0.53 | 25.40 ± 1.57 | 0.34 ± 0.02 | 32.05 ± 1.40 | 13.05 ± 0.26 |
| VanClan3 | 31° 59' 16.8" S 18° 45' 29.6" E | 122 | 21 | | 203.63 | 0.35 | 24.81 ± 2.22 | 0.33 ± 0.02 | | |
| Vonkel | 30° 43' 59.8" S 18° 04' 59.4" E | 301 | 24 | | 142.63 | 0.31 | 12.59 ± 1.01 | 0.44 ± 0.02 | | |
| Wildeperdehoek | 29° 55' 42.6" S 17° 38' 13.2" E | 472 | 7 | 4 | 118.07 | 0.37 | 32.00 ± 2.20 | 0.30 ± 0.01 | 40.00 ± 6.79 | 14.50 ± 0.87 |
| <i>D. pluviialis</i> | | | | | | | | | | |
| Agulhas | 34° 49' 56.9" S 20° 00' 05.9" E | 16 | 4 | 12 | 354.00 | 0.46 | 15.75 ± 2.93 | 0.40 ± 0.03 | 21.25 ± 2.45 | 10.58 ± 0.53 |
| Avontuur | 30° 22' 52.0" S 17° 29' 34.4" E | 66 | 28 | 20 | 93.45 | 0.39 | 12.57 ± 1.09 | 0.52 ± 0.03 | 37.75 ± 1.92 | 14.35 ± 0.36 |
| Bied3 | 32° 08' 51.9" S 19° 12' 42.3" E | 352 | | 14 | 199.48 | 0.38 | | | 46.14 ± 2.68 | 13.29 ± 0.32 |
| Clanwilliam | 32° 10' 11.5" S 18° 48' 21.7" E | 386 | 20 | 14 | 166.40 | 0.34 | 8.77 ± 1.67 | 0.66 ± 0.05 | 46.36 ± 4.23 | 13.43 ± 0.62 |
| Eendekuil | 32° 41' 01.4" S 18° 52' 36.3" E | 124 | 20 | 20 | 243.76 | 0.30 | 15.21 ± 1.75 | 0.50 ± 0.03 | 48.00 ± 3.45 | 13.80 ± 0.54 |
| Hond5 | 30° 23' 22.5" S 17° 30' 32.6" E | 64 | 22 | 13 | 182.53 | 0.41 | 10.66 ± 0.98 | 0.49 ± 0.02 | 39.92 ± 2.74 | 13.69 ± 0.33 |

| | | | | | | | | | | |
|----------------|------------------------------------|-----|----|----|--------|------|--------------|-------------|--------------|--------------|
| Hope1 | 33° 05' 07.5" S 18° 23' 50.4" E | 70 | 22 | 20 | 251.63 | 0.29 | 9.83 ± 0.83 | 0.54 ± 0.02 | 36.45 ± 1.88 | 12.75 ± 0.20 |
| Kners2 | 31° 30' 06.1" S 18° 43' 01.6" E | 139 | | 18 | 124.02 | 0.49 | | | 24.83 ± 2.23 | 11.44 ± 0.42 |
| Kleinzee5 | 29° 45' 26.9" S 17° 15' 17.4" E | 188 | 19 | | 69.08 | 0.49 | 15.67 ± 1.28 | 0.49 ± 0.02 | | |
| Lamberts | 32° 05' 51.5" S 18° 18' 19.6" E | 18 | 20 | 36 | 123.25 | 0.41 | 24.41 ± 2.20 | 0.34 ± 0.02 | 46.97 ± 2.22 | 12.94 ± 0.11 |
| Nieuwoudtville | 31° 23' 16.7" S 19° 10' 44.8" E | 735 | 23 | 20 | 276.18 | 0.32 | 2.12 ± 0.46 | 0.83 ± 0.04 | 50.25 ± 1.69 | 14.85 ± 0.28 |
| Pearlybeach | 34° 39' 42.7" S 19° 29' 15.2" E | 7 | 4 | 8 | 334.53 | 0.30 | 18 ± 5.67 | 0.41 ± 0.06 | 17.00 ± 3.12 | 10.63 ± 0.42 |
| PNStein1 | 29° 18' 36.0" S 17° 07' 05.4" E | 171 | 21 | | 32.23 | 0.50 | 15.35 ± 1.92 | 0.51 ± 0.03 | | |
| Rondebosch | 33° 57' 21.9" S 18° 29' 00.7" E | - | 20 | 21 | 932.46 | 0.23 | 4.65 ± 0.78 | 0.70 ± 0.03 | 31.95 ± 2.43 | 12.19 ± 0.39 |
| Site1 | 32° 05' 18.4" S 19° 23' 13.1" E | 227 | 20 | | 84.25 | 0.51 | 12.90 ± 2.14 | 0.55 ± 0.05 | | |
| Site2 | 32° 08' 25.9" S 19° 15' 58.7" E | 242 | 20 | | 199.48 | 0.38 | 15.70 ± 1.70 | 0.49 ± 0.03 | | |
| Site21 | 31° 29' 58.0" S 18° 43' 02.5" E | 119 | 20 | | 258.25 | 0.37 | 14.95 ± 1.69 | 0.51 ± 0.04 | | |
| Site22 | 31° 45' 20.8" S 18° 38' 59.4" E | 83 | 20 | | 289.67 | 0.33 | 18.50 ± 2.51 | 0.45 ± 0.03 | | |
| Site23 | 31° 59' 35.0" S 18° 46' 08.5" E | 148 | 20 | | 203.63 | 0.35 | 10.25 ± 1.72 | 0.62 ± 0.05 | | |
| Site24.2 | 33° 56' 43.0" S 18° 23' 52.4" E | 424 | 20 | | 932.46 | 0.23 | 2.15 ± 0.87 | 0.89 ± 0.04 | | |
| Site25 | 33° 31' 13.9" S 18° 28' 35.2" E | 180 | 20 | | 361.3 | 0.21 | 1.55 ± 1.34 | 0.92 ± 0.04 | | |
| Site26 | 33° 04' 04.4" S 18° 07' 28.3" E | 68 | 20 | | 239.75 | 0.41 | 9.15 ± 1.99 | 0.67 ± 0.06 | | |
| Site27 | 32° 19' 00.2" S 18° 20' 05.6" E | 7 | 20 | | 182.14 | 0.37 | 9.20 ± 1.78 | 0.65 ± 0.05 | | |
| Site28 | 32° 18' 49.1" S 18° 21' 18.8" E | 11 | 20 | | 182.14 | 0.37 | 8.65 ± 1.69 | 0.66 ± 0.05 | | |
| Site29.2 | 32° 10' 30.4" S 18° 29' 31.1" E | 128 | 20 | | 208.86 | 0.31 | 12.75 ± 1.70 | 0.54 ± 0.03 | | |
| Site30 | 32° 08' 53.8" S 18° 38' 14.1" E | 211 | 20 | | 208.86 | 0.31 | 19.60 ± 2.51 | 0.47 ± 0.04 | | |
| Site31.1 | 32° 09' 40.3" S 18° 34' 20.2" E | 150 | 20 | | 208.86 | 0.31 | 14.25 ± 2.43 | 0.57 ± 0.06 | | |
| Site33 | 33° 06' 14.7" S 17° 59' 55.9" E | 133 | 20 | | 239.75 | 0.41 | 7.75 ± 1.54 | 0.71 ± 0.05 | | |
| Site38 | 33° 16' 07.9" S 18° 19' 46.1" E | 68 | 20 | | 358.63 | 0.23 | 12.20 ± 1.85 | 0.48 ± 0.04 | | |
| Site39 | 33° 24' 27.5" S 18° 24' 50.9" E | 146 | 20 | | 358.63 | 0.23 | 6.80 ± 0.92 | 0.56 ± 0.04 | | |

| | | | | | | | | | | | |
|---------------------|-----------------|------------------------------------|------|----|----|--------|------|--------------|---------------|--------------|--------------|
| | Site5 | 31° 47' 48.5" S 18° 37' 40.3" E | 80 | 20 | | 289.67 | 0.33 | 6.90 ± 1.61 | 0.69 ± 0.04 | | |
| | VanClan1 | 31° 44' 16.7" S 18° 39' 35.5" E | 124 | 19 | | 289.67 | 0.33 | 10.28 ± 1.03 | 0.54 ± 0.03 | | |
| | Varsch | 31° 30' 01.2" S 18° 43' 01.2" E | 123 | 17 | 20 | 124.02 | 0.39 | 10.44 ± 1.15 | 0.58 ± 0.03 | 35.95 ± 3.84 | 14.20 ± 0.66 |
| | Velddrif | 32° 44' 56.5" S 18° 10' 22.9" E | 18 | 20 | 16 | 178.27 | 0.33 | 14.33 ± 1.18 | 0.43 ± 0.02 | 37.19 ± 2.57 | 12.50 ± 0.26 |
| <i>D. polyptera</i> | Platbakkies | 30° 18' 38.1" S 18° 29' 43.6" E | 1061 | 14 | 7 | | | 21.75 ± 2.17 | 0.44 ± 0.02 | 48.00 ± 2.59 | 14.25 ± 0.39 |
| | RoshPinah4 | 27° 43' 25.8" S 16° 42' 55.4" E | 1044 | 16 | | | | 8.79 ± 1.24 | 0.50 ± 0.05 | | |
| | Steinkopfviools | 29° 05' 09.9" S 17° 51' 21.1" E | 809 | 10 | 8 | | | 17.43 ± 2.95 | 0.49 ± 0.03 | 52.38 ± 4.18 | 16.25 ± 0.73 |
| | Suurdam | 30° 38' 09.0" S 18° 25' 47.1" E | 479 | 23 | 15 | | | 17.39 ± 1.64 | 0.47 ± 0.02 | 50.47 ± 2.81 | 15.80 ± 0.63 |
| <i>D. tragus</i> | KamiesC | 30° 14' 20.4" S 17° 55' 44.0" E | 807 | 5 | | | | 36.70 ± 3.22 | 0.003 ± 0.003 | | |
| | Klipfontein | 30° 29' 58.5" S 17° 56' 02.6" E | 504 | 6 | | | | 33.36 ± 7.50 | 0.007 ± 0.007 | | |
| | Nieuw4 | 31° 39' 08.5" S 19° 15' 28.8" E | 693 | 4 | 19 | | | 40.67 ± 4.98 | 0.005 ± 0.005 | 68.42 ± 2.06 | 18.53 ± 0.62 |
| | Spektakel | 29° 41' 45.5" S 17° 39' 13.3" E | 683 | 7 | | | | 44.52 ± 3.19 | 0.00 ± 0.00 | | |
| | Steinridge | 29° 11' 02.7" S 17° 49' 23.5" E | - | 5 | 9 | | | 47.19 ± 7.06 | 0.003 ± 0.003 | 64.89 ± 4.23 | 19.00 ± 0.60 |
| <i>D. cuneata</i> | Kamiesberg | 30° 23' 26.1" S 18° 08' 35.2" E | 1115 | 13 | 20 | | | 16.55 ± 1.61 | 0.10 ± 0.03 | 30.85 ± 1.68 | 13.20 ± 0.24 |
| | Koo | 33° 36' 33.2" S 19° 50' 23.7" E | 1202 | 20 | | | | 17.99 ± 1.47 | 0.10 ± 0.02 | | |
| | Koo-N1 | 33° 26' 31.6" S 19° 50' 17.1" E | 1015 | 5 | | | | 18.07 ± 2.84 | 0.09 ± 0.05 | | |
| | Leliefontein | 30° 18' 36.7" S 18° 04' 28.1" E | - | 7 | | | | 13.12 ± 2.19 | 0.07 ± 0.03 | | |

Table S4.2. Results of linear regressions to test associations of the mean number of ray florets, disk florets and involucre bracts with mean winter precipitation and CV of winter precipitation in populations of *Dimorphotheca sinuata* and *D. pluvialis*. In *D. pluvialis*, results of analyses with mean winter precipitation are shown across all sites as well as excluding site Rondebosch which was an extreme outlier. Similarly, site Kamberg was excluded from the analysis of involucre bracts vs. mean winter precipitation in *D. sinuata*).

| Species | Response variable | Predictor variable | R^2 | F | df | P |
|---------------------|---------------------------------|--|-------|-------|------|-------|
| <i>D. sinuata</i> | | | | | | |
| | Mean number of ray florets | Mean winter precipitation | <0.01 | 0.002 | 1,13 | 0.964 |
| | | CV of winter precipitation | 0.12 | 1.85 | 1,13 | 0.198 |
| | Mean number of disk florets | Mean winter precipitation | 0.12 | 1.73 | 1,13 | 0.211 |
| | | CV of winter precipitation | 0.18 | 2.76 | 1,13 | 0.120 |
| | Mean number of involucre bracts | Mean winter precipitation (all) | 0.17 | 6.03 | 1,30 | 0.020 |
| | | Mean winter precipitation (excl. Kamberg) | 0.03 | 0.77 | 1,29 | 0.386 |
| | | CV of winter precipitation | 0.01 | 0.39 | 1,30 | 0.538 |
| <i>D. pluvialis</i> | | | | | | |
| | Mean number of ray florets | Mean winter precipitation (all) | 0.11 | 1.52 | 1,12 | 0.241 |
| | | Mean winter precipitation (excl. Rondebosch) | 0.25 | 3.64 | 1,11 | 0.083 |
| | | CV of winter precipitation | 0.003 | 0.004 | 1,12 | 0.951 |
| | Mean number of disk florets | Mean winter precipitation (all) | 0.08 | 0.97 | 1,12 | 0.343 |
| | | Mean winter precipitation (excl. Rondebosch) | 0.13 | 1.70 | 1,11 | 0.220 |
| | | CV of winter precipitation | <0.01 | 0.001 | 1,12 | 0.977 |
| | Mean number of involucre bracts | Mean winter precipitation (all) | 0.11 | 1.84 | 1,15 | 0.195 |
| | | Mean winter precipitation (excl. Rondebosch) | 0.26 | 4.83 | 1,14 | 0.045 |
| | | CV of winter precipitation | 0.09 | 1.45 | 1,15 | 0.247 |

Table S4.3. Results of linear regressions to test associations of the difference between the predicted maximum number of central fruit (calculated from the slope of the allometric relationship between ray and disk florets) and the observed number of central fruit with mean winter precipitation and CV of winter precipitation in *Dimorphotheca sinuata* and *D. pluvialis*. The mean number of central fruit failed and mean proportion of central fruit failed were used as dependent variables. Results of analyses with mean winter precipitation are shown across all populations as well as without extreme data outliers: Kamberg (*D. sinuata*) and Rondebosch (*D. pluvialis*).

| Species | Response variable | Predictor variable | R^2 | F | df | P |
|---------------------|-------------------------------------|--|--------|------|------|-------|
| <i>D. sinuata</i> | | | | | | |
| | Mean number of central fruit failed | Mean winter precipitation (all) | 0.13 | 4.47 | 1,30 | 0.043 |
| | | Mean winter precipitation (excl. Kamberg) | 0.01 | 0.27 | 1,29 | 0.609 |
| | | CV of winter precipitation | 0.01 | 0.43 | 1,30 | 0.518 |
| | Proportion of central fruit failed | Mean winter precipitation (all) | <0.01 | 0.03 | 1,30 | 0.868 |
| | | Mean winter precipitation (excl. Kamberg) | 0.0002 | 0.01 | 1,29 | 0.941 |
| | | CV of winter precipitation | 0.04 | 1.12 | 1,30 | 0.299 |
| <i>D. pluvialis</i> | | | | | | |
| | Mean number of central fruit failed | Mean winter precipitation (all) | 0.07 | 0.96 | 1,13 | 0.344 |
| | | Mean winter precipitation (excl. Rondebosch) | 0.20 | 3.03 | 1,12 | 0.107 |
| | | CV of winter precipitation | 0.03 | 0.41 | 1,13 | 0.533 |
| | Proportion of central fruit failed | Mean winter precipitation (all) | 0.03 | 0.36 | 1,13 | 0.557 |
| | | Mean winter precipitation (excl. Rondebosch) | 0.04 | 0.48 | 1,12 | 0.500 |
| | | CV of winter precipitation | 0.03 | 0.35 | 1,13 | 0.566 |

Table S4.4. Results of linear regressions to test associations of mean number of central fruit and mean proportion peripheral fruit with distance to the closest range edge, distance to the northern and eastern range edges, longitude and latitude in populations of *Dimorphotheca sinuata* and *D. pluvialis*. Proportion peripheral fruit in *D. sinuata* was log-transformed. See Methods for description of range edge proximity measurements.

| Species | Response variable | Predictor variable | R^2 | F | df | P |
|---------------------|----------------------------------|---------------------------------|-------|------|------|-------|
| <i>D. sinuata</i> | | | | | | |
| | Mean number of central fruit | Distance to closest range edge | 0.002 | 0.09 | 1,56 | 0.764 |
| | | Distance to northern range edge | 0.004 | 0.21 | 1,56 | 0.646 |
| | | Distance to eastern range edge | 0.001 | 0.04 | 1,56 | 0.833 |
| | | Longitude (x) | 0.004 | 0.23 | 1,56 | 0.636 |
| | | Latitude (y) | 0.001 | 0.07 | 1,56 | 0.799 |
| | Mean proportion peripheral fruit | Distance to closest range edge | 0.001 | 0.07 | 1,56 | 0.786 |
| | | Distance to northern range edge | 0.001 | 0.03 | 1,56 | 0.853 |
| | | Distance to eastern range edge | 0.006 | 0.33 | 1,56 | 0.566 |
| | | Longitude (x) | 0.02 | 0.98 | 1,56 | 0.327 |
| | | Latitude (y) | 0.02 | 1.13 | 1,56 | 0.292 |
| <i>D. pluvialis</i> | | | | | | |
| | Mean number of central fruit | Distance to closest range edge | 0.04 | 1.19 | 1,30 | 0.284 |
| | | Distance to northern range edge | 0.05 | 1.64 | 1,30 | 0.210 |
| | | Distance to eastern range edge | 0.01 | 0.41 | 1,30 | 0.529 |
| | | Longitude (x) | 0.001 | 0.03 | 1,30 | 0.869 |
| | | Latitude (y) | 0.04 | 1.40 | 1,30 | 0.246 |
| | Mean proportion peripheral fruit | Distance to closest range edge | 0.01 | 0.36 | 1,30 | 0.552 |
| | | Distance to northern range edge | 0.02 | 0.73 | 1,30 | 0.398 |
| | | Distance to eastern range edge | 0.01 | 0.36 | 1,30 | 0.555 |
| | | Longitude (x) | 0.001 | 0.02 | 1,30 | 0.895 |
| | | Latitude (y) | 0.03 | 0.81 | 1,30 | 0.376 |

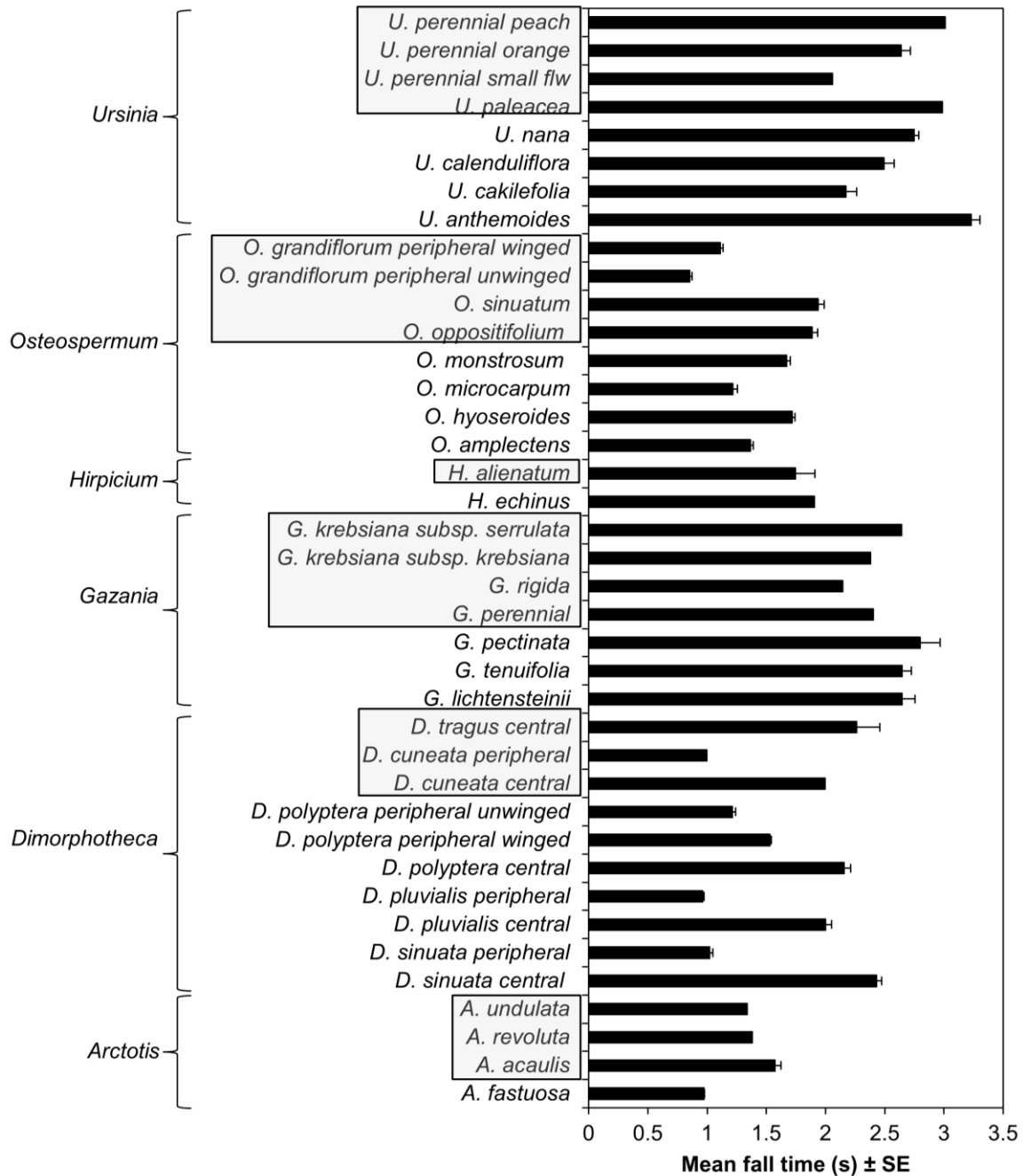


Fig. S5.1. Mean fall time (s) ± SE in annual and perennial (grey blocks) species of seven genera of South African Asteraceae. Fall time is indicated separately for the fruit morphs of heteromorphic species. See Table S1 for sample sizes.

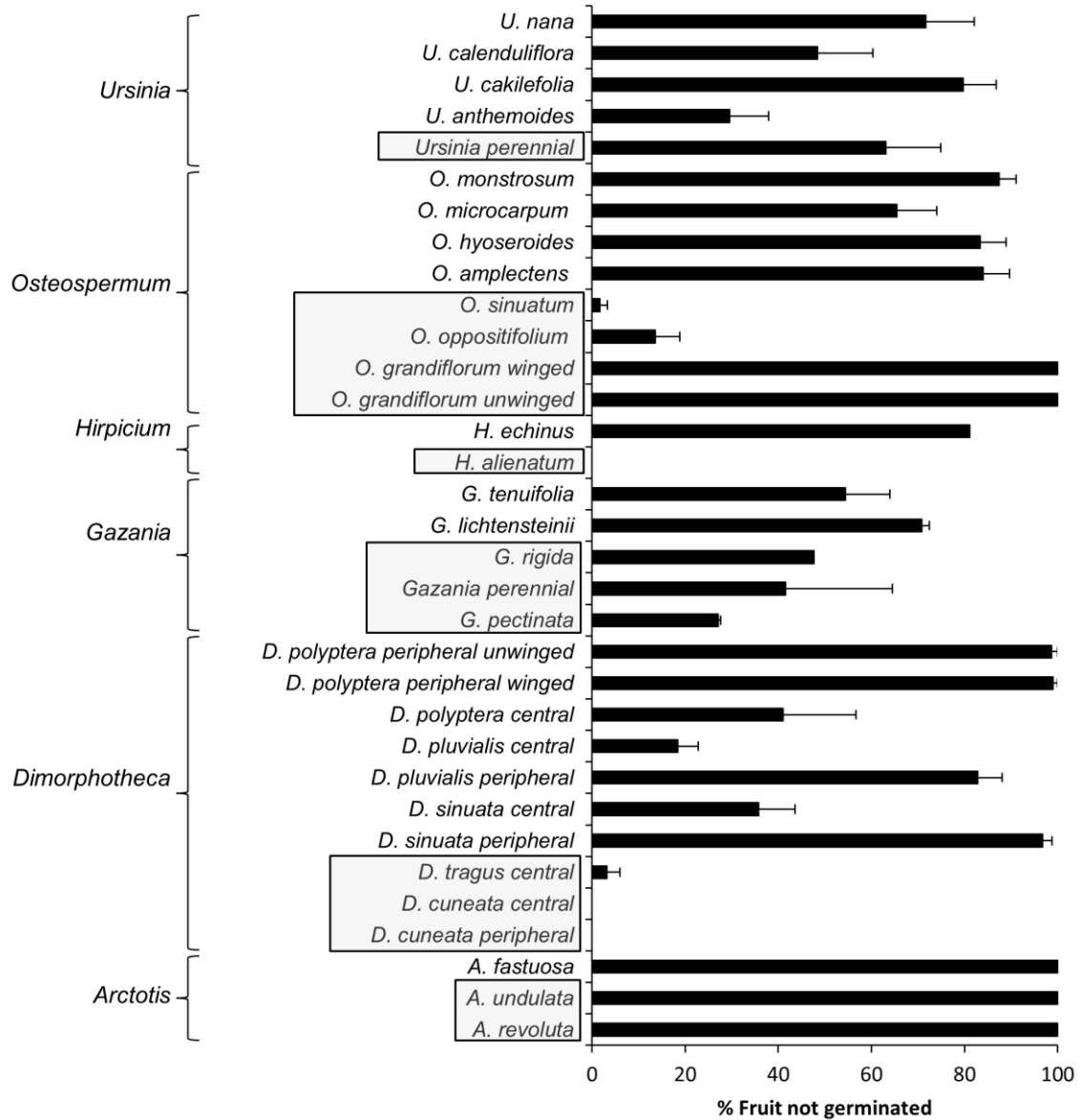


Fig. S5.2. Mean (\pm SE) percentage of viable fruit not germinated within 30 days (measure of dormancy) in populations of annual and perennial (grey blocks) species of six Asteraceae genera. Germination percentages are indicated separately for the fruit morphs of heteromorphic species. See Table S1 for sample sizes.

Table S5.1. Number of populations sampled, and number of fruit sampled per population, for seed dispersal and dormancy in species of annual and perennial South African Asteraceae in six genera (*Arctotis*, *Dimorphotheca*, *Gazania*, *Hirpicium*, *Osteospermum* and *Ursinia*). For heteromorphic taxa (*Dimorphotheca* spp. and *O. grandiflorum*) the number of central (C) and peripheral (P), or winged/unwinged peripheral (WP/UP), fruit is indicated.

| Species | Growth habit | <i>n</i> Dispersal (populations) | <i>n</i> Dormancy (populations) | Population | <i>n</i> Dispersal (individuals) | <i>n</i> Dormancy (individuals) |
|--------------------------|--------------|----------------------------------|---------------------------------|---------------|----------------------------------|---------------------------------|
| <i>A. fastuosa</i> | Annual | 3 | 3 | CalGarContact | 15 | 87 |
| | | | | Oranje4 | 15 | 74 |
| | | | | Wphoek | 15 | 79 |
| <i>A. revoluta</i> | Perennial | 1 | 1 | Spektakelpas | 30 | 45 |
| <i>A. undulata</i> | Perennial | 1 | 1 | Skilpad | 30 | 29 |
| <i>A. acaulis</i> | Perennial | 3 | - | Nieuw3 | 30 | - |
| | | | | PearlyBeach | 15 | - |
| | | | | TinieVersfeld | 25 | - |
| <i>D. sinuata</i> * | Annual | 7 | 14 | Bulletrap | 27 (9P+9C) | 59 (16P+43C) |
| | | | | EkLek4 | - | 61 (21P+40C) |
| | | | | Kamberg | 20 (10P+10C) | 89 (42P+47C) |
| | | | | Kamies | 20 (10P+10C) | 74 (32P+42C) |
| | | | | Klip | 20 (10P+10C) | 55 (10P+45C) |
| | | | | Kliprand1 | - | 88 (41P+47C) |
| | | | | Lamberts | - | 190 (94P+96C) |
| | | | | Moedverloor | 20 (10P+10C) | 55 (18P+37C) |
| | | | | Piket1 | - | 92 (44P+48C) |
| | | | | Richtersveld | - | 54 (13P+41C) |
| | | | | Springbok | - | 82 (35P+47C) |
| | | | | Stein | - | 61 (15P+46C) |
| | | | | Steinkoppie | 20 (10P+10C) | 128 (24P+104C) |
| | | | | VanClan3 | 20 (10P+10C) | 52 (17P+35C) |
| <i>D. pluvialis</i> * | Annual | 4 | 11 | Agulhas | - | 83 (39P+44C) |
| | | | | Avontuur | 20 (10P+10C) | 156 (62P+94C) |
| | | | | Eendekuil | - | 79 (30P+49C) |
| | | | | Hope1 | - | 100 (30P+70C) |
| | | | | Lamberts | - | 89 (40P+49C) |
| | | | | Pearly Beach | - | 87 (37P+50C) |
| | | | | PNStein1 | 23 (12P+11C) | 39 (7P+32C) |
| | | | | Tokai | - | 103 (44P+59C) |
| | | | | VanClan1 | 20 (10P+10C) | 83 (38P+45C) |
| | | | | Varsch | 20 (10P+10C) | 165 (75P+90C) |
| | | | | Velddrif | - | 165 (75P+90C) |
| <i>D. polyptera</i> * | Annual | 3 | 5 | KhubLek4 | - | 36 (8PW+18PU+10C) |
| | | | | Platbakkies | 27 (9PW+9PU+9C) | 61 (22PW+14PU+25C) |
| | | | | RoshPina4 | - | 84 (29PW+18PU+37C) |
| | | | | Site1 | 27 (9PW+9PU+9C) | 53 (16PW+11PU+26C) |
| | | | | Suurdam | 27 (9PW+9PU+9C) | 138 (43PW+46PU+49C) |
| | | | | | | |
| <i>D. tragus</i> * | Perennial | 4 | 4 | Klipfontein | 6 (6C) | 17 (17C) |
| | | | | Nieuw4 | 5 (5C) | 13 (13C) |
| | | | | Spektakel | 4 (4C) | 111 (111C) |
| | | | | KamiesA | 10 (10C) | 97 (97C) |
| <i>D. cuneata</i> * | Perennial | 1 | 1 | Kamberg | 8 (1P+7C) | 14 (5P+9C) |
| <i>G. lichtensteinii</i> | Annual | 3 | 2 | Carminea | 30 | 38 |
| | | | | Tankwa2 | 12 | 21 |

| | | | | | | | | | | |
|--|-----------|-----|----|----------------------|-----------------|---------------|----|-----------|----|-----|
| <i>G. tenuifolia</i> | Annual | 6 | 5 | KhubLek3 | 17 | - | | | | |
| | | | | GrasEk | 30 | 61 | | | | |
| | | | | Kliprand2 | 30 | 26 | | | | |
| | | | | Oranjevallei3 | 30 | 56 | | | | |
| | | | | Roodebergs | 30 | 73 | | | | |
| | | | | Suurdam | 30 | 39 | | | | |
| <i>G. pectinata</i> | Perennial | 2 | 2 | Steinridge | 30 | - | | | | |
| | | | | PearlyBeach | 30 | 49 | | | | |
| <i>G. rigida</i> | Perennial | 1 | - | Rondebosch | 22 | 29 | | | | |
| | | | | Kamies | 12 | - | | | | |
| <i>G. perennial (G. krebsiana subsp. krebsiana?)</i> | Perennial | 1 | 2 | GrasEk | - | 24 | | | | |
| | | | | KhubLek3 | 30 | 27 | | | | |
| <i>G. perennial (G. krebsiana subsp. serrulata?)</i> | Perennial | 1 | - | Griekwastad | 19 | - | | | | |
| | | | | Site1 | 30 | 74 | | | | |
| <i>H. echinus</i> | Annual | 1 | 1 | Kgoedvlakte | 28 | 8 | | | | |
| | | | | Calvinia | 10 | - | | | | |
| | | | | GariesA | 30 | - | | | | |
| | | | | KamiesC | 4 | - | | | | |
| <i>H. alienatum</i> | Perennial | 4 | 1 | EksRd1 | 30 | 89 | | | | |
| | | | | Garies | 27 | 44 | | | | |
| | | | | HondA | 27 | 19 | | | | |
| | | | | Kamies | 30 | 176 | | | | |
| | | | | Naresie | 30 | 81 | | | | |
| | | | | Nuwerus | 20 | 86 | | | | |
| | | | | PlatbakkiesA | 20 | 10 | | | | |
| | | | | Spektakelpas | 30 | 97 | | | | |
| | | | | Springbok | 29 | 28 | | | | |
| | | | | Vonkel | 28 | 39 | | | | |
| | | | | <i>O. amplexens</i> | Annual | 10 | 10 | Buffels | 30 | 30 |
| | | | | | | | | Hond5 | 29 | 14 |
| | | | | | | | | KamiesSKK | 30 | 146 |
| Klip | 30 | 96 | | | | | | | | |
| KZ4 | 29 | 16 | | | | | | | | |
| Spektakelpas | 30 | 98 | | | | | | | | |
| Springbok | 29 | 94 | | | | | | | | |
| SteinC | 24 | 7 | | | | | | | | |
| Wphoek | 30 | 34 | | | | | | | | |
| <i>O. hyoseroides</i> | Annual | 9 | 9 | | | | | Calvinia | 30 | 30 |
| | | | | Clan | 30 | 49 | | | | |
| | | | | Garies-Bitter | 30 | 42 | | | | |
| | | | | GrasEk1 | 29 | 58 | | | | |
| | | | | Hond3 | 30 | 12 | | | | |
| | | | | Klip | 19 | 25 | | | | |
| | | | | Kners2 | 9 | 6 | | | | |
| | | | | Kners-Eskom | 30 | 23 | | | | |
| | | | | Pakhuispas | 21 | 29 | | | | |
| | | | | Van-Nie1 | 30 | 60 | | | | |
| | | | | <i>O. monstrosum</i> | Annual | 10 | 10 | Carminea | 30 | 150 |
| | | | | | | | | GrasEktum | 30 | 93 |
| | | | | | | | | Hond5 | 30 | 66 |
| VanNie2 | 30 | 157 | | | | | | | | |
| <i>O. microcarpum</i> | Annual | 4 | 4 | Peter's Place | 15 (11PW + 4PU) | 13 (10PW+3PU) | | | | |
| | | | | Spektakel | 20 (10PW+10PU) | - | | | | |
| | | | | KamiesA | 20 (10PW+10PU) | - | | | | |
| <i>O. grandiflorum*</i> | Perennial | 3 | 1 | Buffels | 30 | 45 | | | | |
| | | | | EksRd1 | 19 | 15 | | | | |
| | | | | Kam-Spring | 29 | 30 | | | | |
| | | | | Klipfontein | 30 | 19 | | | | |
| | | | | | | | | | | |
| <i>O. oppositifolium</i> | Perennial | 11 | 11 | | | | | | | |
| | | | | | | | | | | |
| | | | | | | | | | | |
| | | | | | | | | | | |
| | | | | | | | | | | |

| | | | | | | |
|--|-----------|----|----|---------------|----|-----|
| | | | | Lutzville | 20 | 73 |
| | | | | PlatbakkiesA | 21 | 23 |
| | | | | PN1 | 22 | 38 |
| | | | | SKK | 30 | 37 |
| | | | | Spektakelpas | 30 | 37 |
| | | | | VanClan2 | 19 | 79 |
| | | | | VRPass | 26 | 87 |
| <i>O. sinuatum</i> | Perennial | 5 | 5 | Buffels | 9 | 9 |
| | | | | EksRd1 | 28 | 60 |
| | | | | Garies | 19 | 14 |
| | | | | Hond2 | 9 | 8 |
| | | | | Site1 | 30 | 23 |
| <i>U. anthemoides</i> | Annual | 10 | 10 | Bied4 | 30 | 93 |
| | | | | Clanwilliam | 27 | 78 |
| | | | | Graaf | 30 | 42 |
| | | | | Moedverloor | 30 | 89 |
| | | | | Pakhuispas | 30 | 38 |
| | | | | Piket1 | 30 | 99 |
| | | | | Spektakelpas | 30 | 137 |
| | | | | StudersPass2 | 30 | 45 |
| | | | | Tokai | 30 | 104 |
| | | | | VanClan3 | 29 | 41 |
| <i>U. cakilefolia</i> | Annual | 6 | 6 | EkLek2 | 30 | 27 |
| | | | | Karkhams | 16 | 11 |
| | | | | Moedverloor | 30 | 45 |
| | | | | NieuwIngang | 30 | 46 |
| | | | | Oranjevallei | 30 | 11 |
| | | | | Skilpad | 49 | 100 |
| <i>U. calenduliflora</i> | Annual | 4 | 4 | Buffels | 30 | 51 |
| | | | | Nababeep2 | 30 | 28 |
| | | | | Okiep2 | 29 | 77 |
| | | | | Spektakelpas | 26 | 70 |
| <i>U. nana</i> | Annual | 5 | 5 | EksRd1 | 30 | 29 |
| | | | | GariesB | 30 | 97 |
| | | | | Nababeep | 7 | 15 |
| | | | | Oranje6 | 30 | 5 |
| | | | | Steinkoppie | 30 | 100 |
| <i>U. perennial (U. chrysanthemoides?)</i> | Perennial | 4 | 4 | CalGarContact | 16 | 18 |
| | | | | KamiesA | 30 | 93 |
| | | | | Spektakelpas | 30 | 39 |
| | | | | StudersPass2 | 22 | 9 |
| <i>U. paleacea</i> | Perennial | 1 | - | Tokai | 30 | - |
| <i>U. perennial (small flower)</i> | Perennial | 1 | - | Grtvadersbos | 30 | - |
| <i>U. perennial (peach flower)</i> | Perennial | 1 | - | Clanwilliam | 29 | - |

*For seed heteromorphic species, the dispersal (fall time) per individual was determined from the mean of approximately 3-5 individual fruits.

Table S5.2. Correlations between fall time and wing loading (the ratio of mass to surface area) of individual fruit in 16 species of South African Asteraceae. Correlations are shown separately for fruit morphs across individuals in heteromorphic *Dimorphotheca* species.

| Species | <i>r</i> | <i>P</i> |
|---|-----------------|-----------------|
| <i>U. anthemoides</i> | -0.48 | < 0.001 |
| <i>U. cakilefolia</i> | -0.82 | < 0.001 |
| <i>U. calenduliflora</i> | -0.47 | < 0.001 |
| <i>U. nana</i> | -0.61 | < 0.001 |
| <i>U. perennial</i> | -0.62 | < 0.001 |
| <i>O. amplectens</i> | -0.36 | < 0.001 |
| <i>O. hyoseroides</i> | -0.72 | < 0.001 |
| <i>O. microcarpum</i> | -0.56 | < 0.001 |
| <i>O. monstrosum</i> | -0.82 | < 0.001 |
| <i>O. oppositifolium</i> | -0.84 | < 0.001 |
| <i>O. sinuatum</i> | -0.83 | < 0.001 |
| <i>D. cuneata</i> (central) | -0.98 | < 0.001 |
| <i>D. pluvialis</i> (peripheral) | -0.10 | 0.673 |
| <i>D. pluvialis</i> (central) | -0.75 | < 0.001 |
| <i>D. polyptera</i> (unwinged peripheral) | -0.20 | 0.421 |
| <i>D. polyptera</i> (winged peripheral) | -0.56 | 0.015 |
| <i>D. polyptera</i> (central) | -0.25 | 0.309 |
| <i>D. sinuata</i> (peripheral) | -0.30 | 0.040 |
| <i>D. sinuata</i> (central) | -0.89 | < 0.001 |
| <i>D. tragus</i> (central) | -0.98 | 0.001 |

Table S5.3. Results of generalised linear models to test the association between dormancy, calculated as [30 – number of days to germination], and fall time of individual fruit in eight populations of six species of southern African Asteraceae.

| Species | Population | Model type | z | P |
|-----------------------------|-------------------|-------------------|-----------------------|----------|
| <i>O. hyoseroides</i> | Wphoek | Zero-inflated | count model: 0.05 | 0.961 |
| | | Poisson | zero-inflation: -1.73 | 0.083 |
| <i>O. microcarpum</i> | VanNie2 | Zero-inflated | count model: 0.05 | 0.441 |
| | | negative binomial | zero-inflation: -1.03 | 0.302 |
| | Hond5 | Zero-inflated | count model: 0.91 | 0.364 |
| | | negative binomial | zero-inflation: 1.52 | 0.128 |
| | GrasEk | Zero-inflated | count model: -0.57 | 0.566 |
| | | negative binomial | zero-inflation: -0.57 | 0.572 |
| <i>O. monstrosum</i> | VanNie1 | Zero-inflated | count model: -0.50 | 0.617 |
| | | Poisson | zero-inflation: -0.69 | 0.492 |
| <i>O. oppositifolium</i> | Lutzville | Negative binomial | -0.94 | 0.349 |
| <i>U. anthemoides</i> | Spektakel | Negative binomial | -0.58 | 0.562 |
| <i>Ursinia</i> perennial sp | Studersplass2 | Negative binomial | -0.88 | 0.380 |