

# Evolution of dispersal traits in a biogeographical context: a study using the heterocarpic *Rumex bucephalophorus* as a model

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## Summary

1. Seed dispersal is crucial in determining the spatial patterns of plant populations, and selection pressure for dispersal varies over different scales. However, few empirical studies have assessed differences in dispersal traits in a biogeographical context.

2. We studied dispersal traits in 46 populations of *Rumex bucephalophorus* from mainland and island locations, and from different habitats to test predictions of how insularity and habitat characteristics affect both dispersability (dispersal capacity and number of dispersible diaspores) and dispersal-distance strategy. We also conducted a greenhouse experiment to compare dispersability of plants in nature and a controlled environment.

3. Dispersability drastically changed when plants were cultivated in the greenhouse, revealing a high phenotypic plasticity for dispersal and showing that the maternal environment directly influences dispersal. However, dispersal-distance strategy, estimated by the production of either long diaspores (LD) or short diaspores (SD), seems to be genetically determined. Dispersability was markedly affected by the habitat in which the plants develop, but the patterns found are not consistent with theoretical predictions. We found two contrasting patterns of dispersal on islands: Atlantic island populations showed a trend to seed monomorphism and mid-dispersal strategy, whilst Mediterranean island populations showed seed heteromorphism and long-dispersal strategy. These contrasting patterns support theoretical predictions that long-distance dispersal evolves in heteromorphic plants, whilst in monomorphic plants only local dispersal evolves. Lastly, we have found a clear mid-dispersal-distance strategy in coastal sands and Atlantic islands; we suggest that the low environmental variation shared by these two zones selects for shorter distances of dispersal.

4. *Synthesis.* Most models describing the evolution of dispersal strategies assume that forces selecting for decreased dispersability also select for decreased dispersal distances. However, in *R. bucephalophorus* dispersal distance and dispersability showed contrasting patterns of variation. The fact that these two traits are differently determined could suggest that they can respond in a different manner to selective pressures.

**Key-words:** dispersal, dispersal distance, habitat stability, islands, phenotypic plasticity, seed heteromorphism, succession

## Introduction

Dispersal is an important process in evolution and speciation, and its role has been underestimated in historical biogeography (Cowie & Holland 2006). Dispersal advantages and disadvantages are well known. Conditions that could benefit from dispersal are the avoidance of inbreeding depression, reduction of competition among kin and escape from

predators (Hamilton & May 1977; Bengtsson 1978; Howe & Smallwood 1982; Olivieri, Michalakis & Gouyon 1995). However, dispersal presents important costs because of reduced survival in a new environment (Bensch *et al.* 1998; Hendry 2004; Nosil, Vines & Funk 2005), or the increase in mortality risk during transport (Alberts & Altmann 1995; Hanski, Alho & Moilanen 2000). Nevertheless, dispersal is a prerequisite for colonizing new habitats and is of utmost importance for metapopulation stability. When traits related to dispersal are variable and more or less determined genetically, selection may operate by reducing or enhancing dispersal of

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populations according to the cost of dispersal (Ronce *et al.* 2001; Cheptou, Carrue & Cantarel 2008). Genetic control of some traits that affect seed dispersal has been confirmed recently in *Arabidopsis thaliana* (Donohue, Polisetty & Wender 2005). Selection could also favour plastic strategies that allow plants to increase or reduce dispersal as the habitat changes (Ronce *et al.* 2005). Such phenotypic plasticity is itself a genetically controlled response to the environment (Murren *et al.* 2001). However, so far, evidence of adaptive plasticity for dispersal traits is scarce in plants (Imbert & Ronce 2001; Ronce *et al.* 2005).

In any species, the optimal level of dispersal should reflect a balance among costs and benefits (Gandon & Michalakis 2001). In some situations, the cost of dispersal is high enough for selection to favour the reduction of dispersal structures as is supposed to occur on Oceanic islands. This idea led Darwin to hypothesize the loss of wings in insects following colonization and establishment on islands (Darwin 1859). Similarly, it has been postulated that effectiveness of dispersal structures of plants will decrease in isolated islands (Carlquist 1965; Cody & Overton 1996; Fresnillo & Ehlers 2008). Island colonists are more likely to have arrived via the most dispersible propagules from mainland populations, so recent island populations will show a high dispersability. However, selection against the loss of diaspores at sea will act to decrease dispersal over time, resulting in older island populations with reduced dispersability (Cody & Overton 1996). In the same way but at a smaller geographical scale and in the context of ecological successions, dispersability may vary between recently founded and older populations, with the latter showing a reduction in dispersability (Olivieri & Gouyon 1985). All these predictions about dispersal evolution assume a genetic basis for dispersal traits, but, as said before, differences in dispersal could also be the expression of phenotypic plasticity. If dispersal is a plastic trait, in the context of successional replacements, it seems optimal to have a low dispersal rate in the colonizing phase of an empty patch, and a higher dispersal rate when habitat deteriorates because of successional events; hence, dispersability should increase rather than decrease with population age (Olivieri & Gouyon 1997; Ronce *et al.* 2005). Knowing whether dispersal ability of a particular species is a genetically based trait or a plastic feature is of utmost importance because predictions from theoretical models differ depending on this question.

On the other hand, most models describing the evolution of dispersal strategies have focused on the evolution of dispersal capacity, although it has been established recently that dispersal distance is also under considerable selective pressure (Hovestadt, Messner & Poethke 2001; Murrell, Travis & Dytham 2002; Bonte, Hovestadt & Poethke 2010). These latter models assume that forces selecting for decreased dispersal capacity could also select for decreased dispersal distances (Murrell, Travis & Dytham 2002; Bonte, Hovestadt & Poethke 2010). In this context and if a genetic basis for dispersal exists, it could be predicted that both insularity and habitat persistence will select against dispersal capacity and

distance, but the opposite pattern would be expected if dispersal is a plastic trait. Despite the existence of theoretical models and experimental studies investigating the evolution of dispersal (Gadgil 1971; Roff 1975; McPeck & Holt 1992; Olivieri, Michalakis & Gouyon 1995; Clobert *et al.* 2001; Mathias, Kisdi & Olivieri 2001; Ronce *et al.* 2005; see Bowler & Benton 2005 for a review; Snyder 2011), there are very few empirical studies throughout wide geographical ranges (Cody & Overton 1996; Cowie & Holland 2006; Darling, Samis & Eckert 2008; Riba *et al.* 2009).

In the course of evolution, some plant species have developed the ability to produce two or more morphologically different diaspores that usually diverge in dormancy, germination behaviour, dispersal traits and/or offspring size (see Imbert 2002 for a review). A difference in dispersal traits among diaspore morphs is one of the most widespread characteristics of such heterocarpic species (McNamara & Quinn 1977; Cheplick & Quinn 1982; Tébar & Llorens 1993; Ruiz de Clavijo 1995; Imbert 2002; Ortiz *et al.* 2009). Theoretical studies about the evolution of dispersal in these species are scarce (Bonte, Hovestadt & Poethke 2010; Snyder 2011), and they point out that a dispersal polymorphism with some seeds being dispersed to long distances is only advantageous in unpredictable environments, whilst dispersal monomorphism with shorter dispersal distances should evolve in more predictable environments (Venable 1985; Snyder 2011). Dispersal capacity in heterocarpic species, that is, the proportion of diaspores that disperse, could be genetically determined (Clay 1982; Olivieri & Gouyon 1985; Cheptou, Carrue & Cantarel 2008), but experimental studies have also revealed the existence of phenotypic plasticity (Baker & O'Dowd 1982; Clay 1982; Imbert & Ronce 2001; Sadeh *et al.* 2009).

*Rumex bucephalophorus* (Polygonaceae) provides excellent opportunities to study geographical variation in dispersal traits. On the one hand, it is heterocarpic and produces dispersible and non-dispersible diaspores, and its dispersability is conditioned by maternal effects (Talavera *et al.* 2010); moreover, the dispersal polymorphism in this species is of particular ecological relevance because it also encompasses a functional separation of both mid and long-distance dispersible diaspores. On the other hand, it inhabits continental areas and islands, and it occurs in quite different habitats. This geographical and biological framework is particularly interesting because it could provide a deeper insight into the interaction of local and regional processes in ecology and evolution (Benard & McCauley 2008). Given that theoretical predictions on dispersal evolution are different if dispersal traits are plastic or genetically determined, we carried out an assessment of phenotypic variation in this species under both controlled and field conditions (Monty & Mahy 2010). Moreover, we studied dispersal in 46 populations of *R. bucephalophorus* from mainland and island locations, and from different habitats to test predictions of how insularity and habitat characteristics affect both dispersability and dispersal distance. If dispersal traits are genetically determined, we will expect a decrease in dispersability in islands and in more stable habitats, but just the opposite patterns if dispersal features are

plastic. In any case, according to theoretical models, we expect that dispersal distance will show similar patterns of variation than those of dispersability.

## Materials and methods

### STUDY SPECIES AND STUDY SITES

*Rumex bucephalophorus* (Polygonaceae) is an annual pioneer species that diverged at 15–16 Ma (Navajas-Pérez *et al.* 2005) in the Mediterranean basin (Talavera 2011) and shows its highest diversity in the western Mediterranean. Plants grow between 0 and 1800 m a.s.l. mainly in coastal habitats, but also in forest clearings, fields and rocky sites. It is a wind-pollinated plant with small mainly hermaphrodite flowers arranged in racemes. Plants show great variability in vegetative and reproductive traits, and the size of the individuals is markedly variable, ranging from only 3–4 cm to 50 cm in height (López González 1990). In some localities, the plants produce a basal leafy rosette from which one or more aerial stems emerge, each of them being topped by a simple raceme; in other areas, plants lack a basal rosette and only present aerial stems. Each plant can produce different types of diaspores that originate from different flower types, and so they are under maternal control (Talavera 2011). The fruit is an achene surrounded by three persistent inner tepals to form the dispersal diaspore. In populations where plants form the rosette of leaves, some flowers may be produced at the axils of these leaves, and the mature diaspores from such flowers are inverted and are buried by the action of contractile roots (buried diaspores, BD). On the aerial stems, three discrete diaspore types which differ markedly in the morphology of the pedicel may be produced: (i) fixed diaspores (FD) show a short and thick stalk, and they become inverted and remain on the plant until senescence and so are not dispersed, (ii) short diaspores (SD) show a short but thin stalk that detaches easily and so are dispersed; they can be carried by wind for short-medium distances or are simply dispersed by barochory, (iii) long diaspores (LD) show a concave and curved long stalk that detaches easily and functions as a wing, and so they can be dispersed by wind over longer distances (pictures of every diaspore type can be seen in Talavera *et al.* 2011). Diaspores of *R. bucephalophorus* do not differ in dormancy (M. Talavera, unpubl. data). On the other hand, diaspore types are not homogeneously distributed along aerial stem: FD diaspores are produced mainly at the first nodes of the plants, and their production decreases from the base to the apex of the raceme, whilst LD and SD diaspores show the reverse trend (Talavera *et al.* 2010; Talavera 2011).

In addition, the two dispersible diaspores, LD and SD, differ in terminal velocity (mean of  $1.49 \pm 0.04 \text{ m s}^{-1}$  for LD and  $2.52 \pm 0.1 \text{ m s}^{-1}$  for SD), and in the mean dispersal distances ( $82.3 \pm 2.7 \text{ cm}$  and  $58.4 \pm 2.6 \text{ cm}$ ) measured in a wind tunnel with a wind speed of  $2.5 \text{ m s}^{-1}$  and a height of 25 cm. Although long-distance seed dispersal is notoriously difficult to quantify, previous modelling approaches showed that wind velocity, seed release height, terminal velocity and vegetation height are crucial determinants of dispersal distances and dispersal potential (Soons *et al.* 2004). Moreover, wind updrafts provide the key mechanism for long-distance dispersal with uplifting events occurring only when vertical wind velocity exceeds seed terminal velocity (Nathan *et al.* 2002). Thus, although in basis on our data, distances reached in nature are difficult to be predicted, it seems reasonable to assume that LD diaspores will reach longer distances than SD and that the probability of long-distance dispersal events will be higher for LD diaspores.

To discover whether dispersability and dispersal distance vary in a biogeographical context, we sampled a total of 46 populations of *R. bucephalophorus* in the western Mediterranean and Atlantic region (Table 1). At a small geographical scale, we sampled *R. bucephalophorus* in diverse habitats that constitute early stages of succession. These habitats were fixed coastal sands, forest clearings, fields and rocky areas (Table 1). Forest clearings and field habitats were unstable sites because of human influences. In fact, the clearings are very fragmented habitats caused by forest management, and the field habitats were at the roadsides or corresponded to temporarily unused agricultural lands. In contrast, fixed coastal sands and rocky areas are relatively more stable sites with little influence of human activities. However, fixed coastal sands where *R. bucephalophorus* develops have become fragmented habitats in the last decades. Density of *R. bucephalophorus* plants varied among habitats: fields showed the highest (about 40 plants  $\text{m}^{-2}$ ), followed by forest clearings and coastal sands (about 20 plants  $\text{m}^{-2}$ ), and lastly, rocky sites showed the lowest density (about 2 plants  $\text{m}^{-2}$ ).

At a large geographical scale, our survey included 29 mainland populations (19 from southern Europe and 10 from North Africa) and 17 island populations (6 from western Mediterranean and 11 from Atlantic islands; Table 1). Molecular analyses indicate that populations on Atlantic islands are in general younger than mainland or Mediterranean ones (Talavera *et al.* 2011). The Mediterranean and Atlantic islands differ in many aspects, such as origin, age, climate and vegetation. All populations from Mediterranean islands and most from the mainland localities have Mediterranean climates, whilst Atlantic islands have climate ranging from subtropical to tropical. Despite sampling effort, we could not find *R. bucephalophorus* from coastal sands in Atlantic islands or from rocky areas in Mediterranean islands.

### METHODS

In each sampled population between 8 and 12 plants were randomly collected and on one stem of each, all the diaspores were counted. The diaspores were assigned to the four different classes described above: buried (BD), fixed (FD), short (SD) and long (LD). For each plant, we considered two measures of dispersability, named the total number of dispersible diaspores (LD + SD) and the dispersal capacity; this was calculated by the expression 'Dispersal Capacity = LD + SD/Total Diaspores' that indicates the proportion of diaspores that are dispersed in relation to total diaspore production per plant. Given that the two types of dispersible diaspores (SD and LD) do not usually co-occur in the same plant, we have considered two dispersive strategies differing in distance that we have called mid-dispersal and long-dispersal. *Rumex bucephalophorus* plants were assigned to one of these two alternative dispersal strategies.

Differences in dispersability among populations may result from genetic differences or from phenotypic plasticity related to some environmental factors. To assess the importance of phenotypic plasticity in dispersal traits of *R. bucephalophorus*, plants from two contrasting populations (Mamora, Morocco, in forest clearings and Carrapateira, Portugal, in coastal sand dunes; see Table 1) were randomly collected. Diaspore production was quantified in these plants, and their dispersal capacity was calculated as described above. All diaspores from 30 mother plants from each population were gathered and mixed; then, about 100 diaspores were randomly collected and sown. The emerged seedlings were transferred to individual plastic pots (filled with a mixture of peat and perlite) and maintained in a

**Table 1.** Sampled populations of *Rumex bucephalophorus*, diaspore types (BD, buried diaspores; FD, fixed diaspores; SD, short diaspores; LD, long diaspores), collection number, habitat, altitude and coordinates

Site and locality	Collection number and collector	Diaspore types	Habitat and elevation	Coordinates
<b>Mainland</b>				
Algeria. Kef Fatima	242/07; EV	SD, LD	Coastal sands, 2 m	36°54'N/7°02'E
Algeria. AïnBarbâr	241/07; EV	FD, LD	Coastal sands, 3 m	36°51'N/7°48'E
Morocco. Middle Atlas. Azrou	61/06; ST	FD, LD	Fields, 1457 m	33°31'N/5°18'W
Morocco. Al-Hoceima-Nador	101/07; MT	BD, FD, LD	Coastal sands, 90 m	35°11'N/3°19'W
Morocco. Taza-Fez	142/07; MT	FD, LD	Fields, 570 m	34°03'N/4°26'W
Morocco. Tanhrent-Tetuan	20/07; MT	BD, FD, LD	Fields, 112 m	35°46'N/5°31'W
Morocco. Chaouen-OuedLaou	46/07; MT	FD, LD	Coastal sands, 3 m	35°24'N/5°07'W
Morocco. High Atlas. Oukaimeden	89/08; MT	FD, LD	Rocks, 2167 m	31°14'N/7°48'W
Morocco. Middle Atlas. Beni-Mellal	71/08; MT	FD, LD	Fields, 1275 m	32°16'N/6°17'W
Morocco. La Mamora	184/06; ST	BD, FD, LD	Forest clearings, 154 m	34°03'N/6°33'W
Portugal. Minho. Viana do Castelo	267/06; ST	FD, LD	Coastal sands, 5 m	41°43'N/8°52'W
Portugal. Estremadura. Peniche	223/07; ER	BD, FD, LD	Coastal dunes, 6 m	39°20'N/9°21'W
Portugal. Algarve. Carrapateira	240/06; ST	BD, FD, LD	Coastal dunes, 20 m	37°11'N/8°54'W
Portugal. BaixoAlentejo. Sines	249/06; ST	BD, FD, LD	Forest clearings, 204 m	38°01'N/8°46'W
Spain. Almería. Tahal	222/07; JP	FD, LD	Fields, 1050 m	37°13'N/2°16'W
Spain. Badajoz. Don Benito	12/07; MJG	BD, FD, LD	Fields, 279 m	38°54'N/5°52'W
Spain. Cádiz. Zahara de los Atunes	1/10; MA	FD, LD	Forest clearings, 400 m	36°06'N/5°46'W
Spain. Cádiz. San Roque	357/06; MT	FD, SD	Coastal sands, 3 m	36°17'N/5°16'W
Spain. Córdoba. Carcabuey	227/07; PLO	FD, LD	Calcareous rocks, 658 m	37°26'N/4°16'W
Spain. Granada. Guadix	221/07; JP	FD, LD	Fields, 850 m	37°36'N/3°12'W
Spain. Huelva. Hinojos	368/06; MT	BD, FD, LD	Forest clearings, 92 m	37°17'N/6°25'W
Spain. Huelva. Almonte	369/06; MT	BD, FD, LD	Forest clearings, 60 m	37°13'N/6°22'W
Spain. Lugo. San Cosme	306/06; ST	FD, SD	Coastal sands, 11 m	43°33'N/7°11'W
Spain. Málaga. Estepona	362/06; MT	SD	Coastal sands, 5 m	36°20'N/5°14'W
Spain. Málaga. Marbella	363/06; MT	SD, LD	Coastal sands, 2 m	36°29'N/4°46'W
Spain. Pontevedra. Moaña	288/07; SC	FD, SD	Fields, 30 m	42°16'N/8°45'W
Spain. Cáceres. Plasencia	226/07; AC	FD, LD	Forest clearings, 360 m	40°02'N/6°06'W
Spain. Segovia. Villar de Sobrepeña	225/07; ER	FD, LD	Fields, 1050 m	40°56'N/2°10'W
Spain. Sevilla. El Gandul	370/06; MT	FD, LD	Fields, 86 m	37°19'N/5°47'W
<b>Mediterranean islands</b>				
Balearic Islands. Formentera. Migjorn	2/10; MLB	FD, LD	Coastal sands, 4 m	38°41'N/1°28'E
Corsica. Ostriconi	3/09; KT	FD, LD	Coastal sands, 30 m	42°39'N/9°04'E
Sardinia. Oloni-Seni	213/09; MT	FD, LD	Field, 863 m	39°50'N/9°18'E
Sardinia. S. Antioco Island. Calasseta	283/09; MT	FD, LD	Forest clearings, 1 m	39°05'N/8°21'E
Sardinia. S. Antioco Island. Cussorgia	282/09; MT	FD, LD	Coastal sands, 4 m	39°06'N/8°23'E
Sicily. Messina	10/08; KT	SD, LD	Fields, 540 m	38°12'N/15°30'E
<b>Atlantic islands</b>				
Canary Islands. El Hierro. Mocanal	57/09; MT	FD, SD	Fields, 543 m	27°49'N/17°56'W
Canary Islands. Fuerteventura. La Oliva	22/09; MT	FD, LD	Volcanic rocks, 272 m	28°37'N/13°55'W
Canary Islands. Gran Canaria. Cruz de Tejeda	38/09; MT	FD, LD	Fields, 1488 m	28°03'N/15°36'W
Canary Islands. Gran Canaria. Guayadeque	42/09; MT	BD, FD, LD	Fields, 907 m	27°56'N/15°30'W
Canary Islands. La Gomera. Garajonay	59/09; MA	BD, FD, SD, LD	Forest clearings, 1300 m	28°06'N/17°14'W
Canary Islands. Lanzarote. Monte Corona	4/09; MT	FD, LD	Volcanic rocks, 409 m	29°11'N/13°29'W
Canary Islands. Lanzarote. Monte Tinache	9/09; MT	FD, LD	Volcanic rocks, 346 m	29°03'N/13°40'W
Canary Islands. Tenerife. Anaga	45/09; MT	FD, SD	Forest clearings, 577 m	28°32'N/16°12'W
Canary Islands. Tenerife. Icod	49/09; MT	FD, SD	Fields, 447 m	28°21'N/16°42'W
Madeiran archipelago. Madeira	MS5057; MS	FD, SD	Volcanic rocks, 1720 m	32°44'N/16°56'W
Madeiran archipelago. Porto Santo	195/07; MS	FD, SD	Volcanic rocks, 280 m	33°05'N/16°18'W

EV, E. Vela; ST, S. Talavera; MT, M. Talavera; ER, E. Rico; JP, J. Peña; MJG, M. J. Gallego; MA, M. Arista; PLO, P. L. Ortiz; SC, S. Castroviejo; AC, A. Crespo; KT, K. Tremetsberger; MLB, M. L. Buide; MS, M. Sequeira.

greenhouse and watered daily. These plants were grown on to fruit production, and their diaspore production was quantified and their dispersal capacity calculated.

A common way in which habitat conditions can affect plant dispersal is through their influence on seed size and mass, and the subsequent effects of seed size on dispersal ability (Greene

& Johnson 1990; Meyer & Carlson 2001). Thus, given that diaspore mass is decisive for dispersal in many anemochorous species, in most populations we collected ripe dispersible diaspores (both short and long) from 5 to 12 plants. For these diaspores, we measured mass by using an electronic balance with a precision of 0.0001 g.

## STATISTICAL ANALYSIS

To test differences in dispersal capacity of the plants from Mamora and Carrapateira according to growing conditions (field versus greenhouse), we used a GLM with population and growing conditions as main effects, and considering their interaction. Moreover, differences in diaspore production (total, and FD and LD separately) for plants of both populations according to growing conditions were tested by using a GLM analysis with population and growing conditions as the main effects, and considering their interaction. When the GLMs showed significant differences, the means of treatments were compared using *t*-tests based on the standard errors calculated from the specific model. To test the relationship between total diaspore production and dispersal capacity, Pearson correlation was calculated.

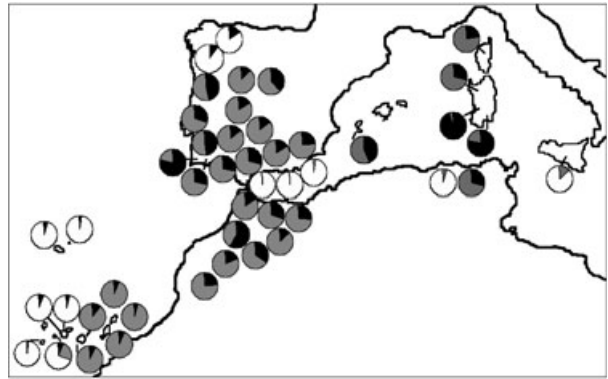
Differences among sites (mainland, Atlantic islands and Mediterranean islands) or habitats (forest clearings, fields, fixed coastal sands and rocks) in the measures of dispersability, diaspore mass and dispersal-distance strategy were tested by means of an additive model with habitat and site as main factors, as it was impossible to test the interaction between them because of all habitats not being represented in all sites. Dispersal capacity was analysed by using a binomial model and the total number of dispersible diaspores by mean of Poisson models. Differences in diaspore mass could result from differences in mass of the two diaspore types that disperse (SD and LD) because they were not both present in all populations. So, we performed a one-way ANOVA to test differences in mass of each diaspore type. Dispersal-distance strategy was categorized as a binomial variable, with plants assigned to one of two categories (0, mid-dispersal strategy, 1, long-dispersal strategy). To know whether both strategies show any geographical patterns, we used an additive model with habitat and site as main factors, and with dispersal-distance strategy as the variable response.

All *P*-values were calculated with marginal (Type III) tests for significance. When the GLMs showed significant differences, the means of treatments were compared using *t*-tests based on the standard errors calculated from the specific models. To control for type I error in the analysis, we used sequential Bonferroni test to adjust the significance level.

## Results

From the 46 populations sampled, only 11 produced BD diaspores: nine were found on the mainland, and two on Atlantic islands. Populations that produce BD diaspores were mainly growing on coastal sands and to a lesser extent in forest clearings. All populations with BD diaspores also produced FD and LD diaspores. With regard to the aerial diaspores, most populations (35) developed FD and LD diaspores, nine produced FD and SD, three had exclusively dispersible diaspores (SD and LD), and one produced only one type (SD) of diaspore (Fig. 1; Table 1).

Dispersal capacity was markedly variable among populations (Wald  $\chi^2 = 3248.4$ ,  $P < 0.001$ ), ranging from 50 to 100% in most populations, whilst only four populations showed a lower dispersal capacity (4.86%, 21.8%, 22.3% and 42.8%; Fig. 1). The production of dispersible diaspores also showed significant differences among populations ( $F_{45,341} = 12.7$ ,  $P < 0.001$ ). Diaspore mass was very variable among populations ( $F_{42,264} = 17.56$ ,  $P < 0.001$ ), ranging from 0.5 to

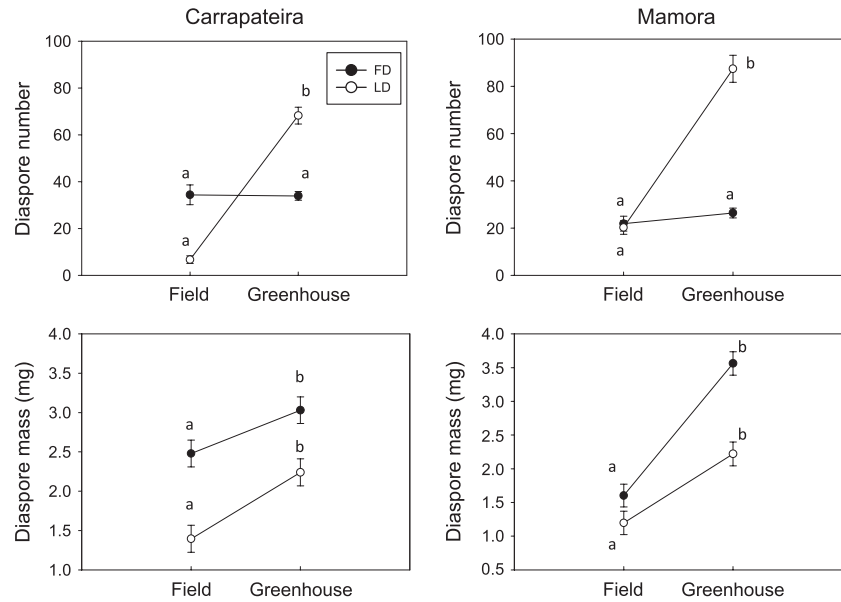


**Fig. 1.** Distribution of 46 *Rumex bucephalophorus* populations showing the proportions of fixed diaspores (black), short diaspores (white) and long diaspores (grey).

2 mg in most cases; only three populations produced heavier diaspores. The two types of dispersal diaspores differed significantly in mass ( $F_{1,1241} = 151.55$ ,  $P = 0.001$ ): LD diaspores were lighter ( $1.19 \pm 0.02$  mg) than SD diaspores ( $1.94 \pm 0.06$  mg).

### AMONG POPULATION DIFFERENTIATION FOR DISPERSAL

Total diaspore production of plants markedly increased when they were grown in the greenhouse (Wald  $\chi^2 = 86.15$ , 1 d.f.,  $P < 0.001$ ). Plants from Mamora produced a mean of  $42.1 \pm 9.6$  diaspores in the field and  $113.8 \pm 5.5$  in the greenhouse, and those from Carrapateira produced  $41.1 \pm 8.2$  and  $102.2 \pm 3.7$ , respectively; there were no differences between populations in diaspore production (Wald  $\chi^2 = 0.79$ , 1 d.f.,  $P = 0.38$ ). Dispersal capacity also increased when plants were grown in the greenhouse (Wald  $\chi^2 = 96.40$ , 1 d.f.,  $P < 0.001$ ), and a significant positive correlation between total diaspore production and dispersal capacity was found ( $r = 0.575$ ,  $n = 157$ ,  $P < 0.001$ ). Mean dispersal capacity of Mamora plants in the field was  $48.7 \pm 5.1\%$ , and this increased to  $74.6 \pm 2.9\%$  in the greenhouse; similarly, dispersal capacity of Carrapateira plants increased from  $15.9 \pm 4.3\%$  in the field to  $64.1 \pm 2\%$  in the greenhouse. In the two growing conditions (greenhouse versus nature), Mamora plants showed higher dispersal capacity than Carrapateira plants ( $P < 0.005$  in all comparisons). Taking into account the two types of diaspores, differences between field and greenhouse plants were found exclusively in the production of dispersible diaspores (Wald  $\chi^2 = 101.23$ , 1 d.f.,  $P < 0.0001$ ). In fact, in both populations, the number of non-dispersible diaspores per plant was similar in the field and in the greenhouse, whilst the production of LD diaspores increased notably in the greenhouse (Fig. 2). In both populations, diaspore mass showed an increase for greenhouse-grown plants ( $P < 0.0001$  in both comparisons); this increase was found in both LD and FD diaspores and in both populations, but it was higher in Mamora where diaspores were lighter in nature (Fig. 2).



**Fig. 2.** Production and mass of fixed and long diaspores of *Rumex bucephalophorus* from two populations (Carrapateira in coastal sands and Mamora in forest clearings) growing in the field and in greenhouse conditions. Estimated means and standard errors are shown. Means followed by different small case letters indicate significant differences between field and greenhouse conditions within each population ( $P < 0.05$ ).

#### HABITATS

Dispersal capacity of populations varied markedly among habitats (Wald  $\chi^2 = 429.8$ ,  $P < 0.001$ ) with plants from forest clearings showing the lowest dispersal capacity and those from rocks and fields the highest (Fig. 3). The production of dispersible diaspores also differed among habitats (Wald  $\chi^2 = 217.1$ ,  $P < 0.001$ ). The lowest number of dispersible diaspores was found in forest clearings and the highest in fields. Diaspore mass varied markedly among habitats (Wald  $\chi^2 = 59.7$ ,  $P < 0.001$ ), diaspores from fixed coastal sands being the heaviest, whilst diaspores from rocks were the lightest (Fig. 3). In all habitats, plants showing the long-dispersal strategy were predominant, ranging from 65.52% in rocks to 91.29% in forest clearings; however, dispersal-distance strategy varied significantly among habitats (Wald  $\chi^2 = 32.3$ ,  $P < 0.001$ ). Plants showing the mid-dispersal strategy were much more abundant in coastal sands, whilst those showing long-dispersal strategy were predominant in the remaining habitats (Fig. 3).

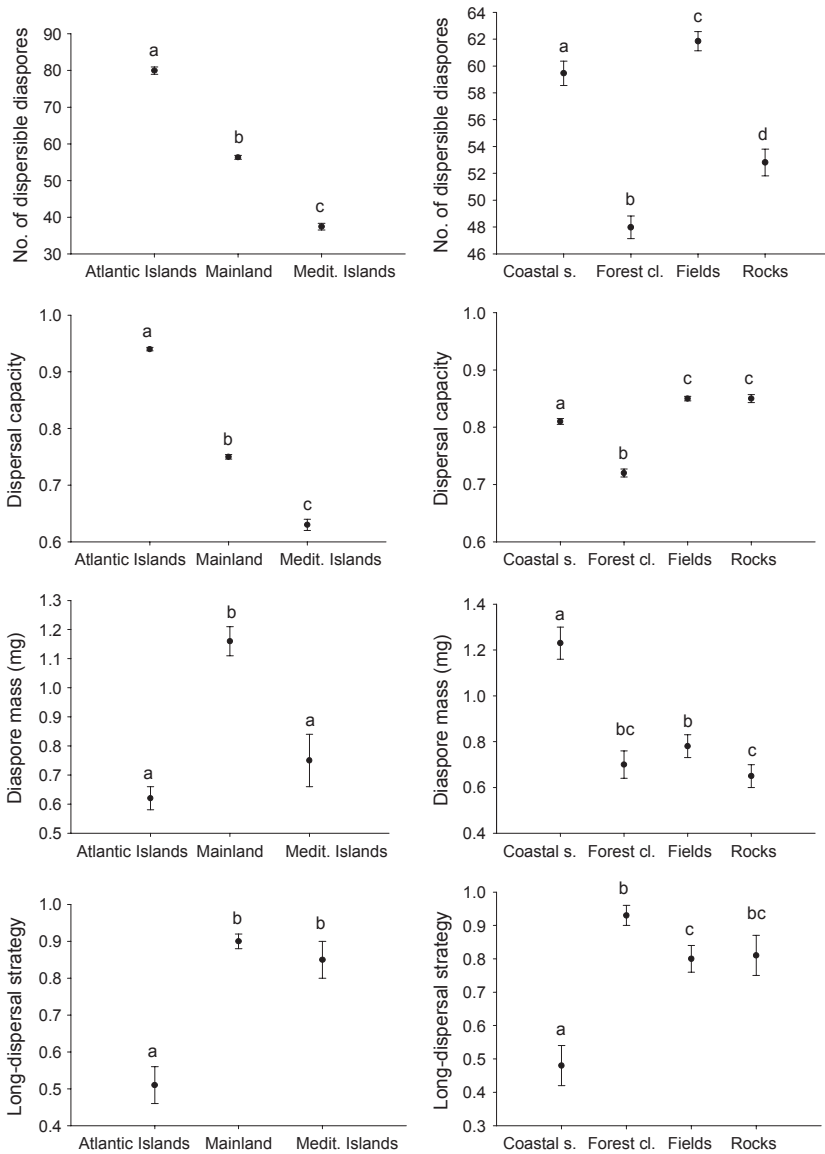
#### ISLANDS VERSUS MAINLAND

Variation in dispersal capacity among populations of *R. bucephalophorus* showed a clear and significant geographical pattern (Wald  $\chi^2 = 1198.7$ ,  $P < 0.001$ ); the lowest dispersal capacity was found in populations from Mediterranean islands, and the highest in those from Atlantic islands (Fig. 3). Marked differences among sites were found in the number of dispersible diaspores (Wald  $\chi^2 = 867.9$ ,  $P < 0.001$ ); with the highest in Atlantic islands and the lowest in Mediterranean ones (Fig. 3). Diaspore mass also showed significant differences among sites (Wald  $\chi^2 = 82.49$ ,  $P < 0.001$ ); populations of both Atlantic and Mediterranean islands produced the lightest diaspores, and those of mainland were the heaviest (Fig. 3). Dispersal-distance strategy varied among sites (Wald  $\chi^2 = 36.05$ ,  $P < 0.001$ ); long-dispersal

strategy being significantly less frequent in Atlantic islands than in both Mediterranean islands and the mainland (Fig. 3).

#### Discussion

Most *R. bucephalophorus* populations produced both non-dispersible diaspores to remain at the site and dispersible diaspores to reach new locations. The two measures of dispersability (dispersal capacity and production of dispersible diaspores) were markedly variable among populations and plants. Theoretical studies have suggested that differences in dispersability among populations may result from genetic differences (Olivieri, Couvet & Gouyon 1990; Olivieri, Michalakis & Gouyon 1995) or from phenotypic plasticity related to some environmental factors (Ronce *et al.* 2005) that, in turn, is a genetically controlled response to environment (Murren *et al.* 2001). The fact that plants from the Mamora and Carrapateira populations markedly increased diaspore mass and diaspore production when growing in the greenhouse is no doubt a consequence of favourable conditions in cultivation. However, these plants only increased the production of LD whilst maintaining that of FD; as a result, their dispersal capacity markedly increased. This result reveals a high phenotypic plasticity for dispersal, and it shows that the maternal environment influences dispersal directly (Thiede & Augspurger 1996; Donohue 1999; Imbert & Ronce 2001). In other heterocarpic species, this plastic response has been attributed, at least in part, to developmental constraints, because each diaspore morph occurs in a different position on the plant (Imbert, Escarré & Lepart 1999; Sadeh *et al.* 2009). In *R. bucephalophorus*, the proportion of FD diaspores usually decreases from the base to the apex of the raceme and that of LD diaspores shows the reverse pattern, but some FD diaspores can also be found in the apical third of the inflorescence and LD in the basal third (Talavera *et al.* 2010). Thus,



**Fig. 3.** Number of dispersible diaspores, dispersal capacity, diaspore mass and dispersal distance strategy of *Rumex bucephalophorus* populations according to the sites (Atlantic islands, mainland and Mediterranean islands) and to the habitat type (fixed coastal sands, forest clearings, fields and rocks). Estimated means and standard errors are shown. Means followed by different small case letters indicate significant differences between sites or habitats ( $P < 0.05$ ).

developmental constraints do not seem to be a major cause of phenotypic plasticity for dispersal in this species.

On the other hand, plants from the Mamora forest clearings showed a higher dispersal capacity than those from Carrapateira coastal sands, both in nature and in the greenhouse. There are only a few studies in the context of dispersal, in which phenotypic differentiation among populations was also studied in a common garden experiment (Mix *et al.* 2006; Cheptou, Carrue & Cantarel 2008; Riba *et al.* 2009). The experiment we performed on *R. bucephalophorus* populations indicates that differences between populations were maintained regardless of growing conditions. This could suggest that part of the observed variability in natural conditions is genetically based (Imbert, Escarré & Lepart 1999; Cheptou, Carrue & Cantarel 2008; Lázaro & Traveset 2009). However, differences in dispersal capacity between populations in greenhouse conditions could also be due to maternal effects, that is, the effects of maternal phenotype or maternal environment in the offspring

phenotype over and above the direct effect of transmitted genes (Marshall & Uller 2007). In *R. bucephalophorus*, dispersability is influenced by marked maternal effects that even affect second generation progeny (Talavera *et al.* 2010), which suggests that differences between populations in the greenhouse could also be a plastic response to environment suffered by mother plants in the field.

In contrast, the production of either LD or SD diaspores seems to be genetically determined, as the plants in both field and greenhouse maintained the same type of dispersible diaspores. Although in the present study, we used two populations with the same type of dispersible diaspores (LD), results from 2-year cultivation of 20 populations with both dispersal strategies represented (Talavera 2011) support this assumption. Given that both diaspore types differ in dispersal distances, we can conclude that in *R. bucephalophorus*, dispersal-distance strategy seems to be genetically determined.

## HABITATS

The wide survey of *R. bucephalophorus* natural populations has shown that dispersability and diaspore mass are markedly affected by the habitat in which the plants develop. *Rumex bucephalophorus* is a pioneer species that is subjected to successional replacement. Assuming that dispersability is a plastic trait in this species, theoretical models in the context of ecological succession predict an increase in the dispersal rate with population age (Olivieri & Gouyon 1997; Ronce *et al.* 2005). We have found the lowest dispersability in forest clearings, whilst the highest were found in fields and rocks. We do not know how old the studied populations are, but we can expect those in unstable sites to be younger. In this way, the contrasting patterns of dispersal capacity found in forest clearings and fields, the most unstable habitats, are not consistent with theoretical predictions, and this suggests that other environmental factors are affecting dispersability. Interspecific competition, recruitment rates and disturbance regime have been proposed to change during colonization modifying selective pressures on plastic dispersal strategies (Ronce *et al.* 2005).

Among the studied habitats, the mid-dispersal strategy was mainly found in fixed coastal sands, whilst the long-dispersal strategy was predominant in forest clearings, fields and rocks. Differences in diaspore mass among habitats seem to be associated with differences in dispersal-distance strategy, as SD diaspores are heavier than LD diaspores. We have not found any pattern in the distribution of the dispersal-distance strategies related to habitat fragmentation or habitat stability because of human influences. A very distinctive feature of coastal sands, in relation to the other habitats, is a lower climatic unpredictability with severe weather events, such as droughts or frosts, being less probable. This kind of habitat stability related to climate could select for the mid-dispersal strategy.

## ISLANDS AND MAINLAND

We have found two contrasting patterns of dispersability on islands: populations of Mediterranean islands showed both the lowest dispersal capacity and the lowest production of dispersible diaspores and those of Atlantic islands had the highest ones. The existence of these two different patterns does not support theoretical predictions about the evolution of dispersability in islands. Although *R. bucephalophorus* is a heterocarpic species, plants in Atlantic islands produced such a high proportion of dispersible diaspores (mean 94%) that they behave almost like monomorphic plants. In contrast, on Mediterranean islands and to a lesser extent on the mainland, plants showed a clear polymorphic strategy producing a high proportion of diaspores to disperse and a considerable proportion to stay at site. Diaspore heteromorphism has been traditionally considered a bet-hedging strategy that is adaptive in unpredictable environments (Venable 1985). In temporally, variable environments selection favours individuals that produce offspring differing in their dispersal, germination speed or life history; such strategy reduces temporal variation in survival rates, which in turn increases the long-term rate of

population growth (Venable 1985; Venable *et al.* 1987). Additionally, theoretical models show that dispersal heteromorphisms are expected in highly unpredictable environments and monomorphic dispersal in more predictable ones (Venable 1985; Snyder 2011). In concordance, heterocarpic species typically occur in either dry or Mediterranean habitats (Imbert 2002). Mediterranean islands and mainland areas of this study show typically Mediterranean climate that is very unpredictable with high interannual variability (Rodó & Comín 2001). In contrast, the subtropical Atlantic islands are under the direct influence of the trade winds leading to fog precipitation, which makes the climate quite predictable (García *et al.* 2001; Prada *et al.* 2009). Our results support theoretical models with dispersal heteromorphism found in temporally variable Mediterranean island and mainland populations, and with a trend to monomorphism in more stable Atlantic islands.

Atlantic islands also showed a different strategy of dispersal distance, because populations producing mid-dispersal-distance diaspores (SD) were especially frequent. The geographic variation in the proportions of plants with different dispersal capabilities may reflect adaptation to different environmental regimes (Venable, Dyreson & Morales 1995; Telenius & Torstensson 1999). Taking into account the two measures of dispersal, we have found that Atlantic island populations showed seed monomorphism and mid-dispersal strategy, whilst Mediterranean island and mainland populations showed seed heteromorphism and long-dispersal strategy. These contrasting patterns support theoretical predictions that long-distance dispersal evolves in heteromorphic plants, whilst in monomorphic plants only local dispersal evolves (Snyder 2011). Dispersal capacity and dispersal distance determine gene-flow (Lenormand 2002; Garant, Forde & Hendry 2007) and may influence local adaptation and evolution (Bonte, Hovestadt & Poethke 2010). The mid-distance dispersal of Atlantic island populations may strongly favour processes of local adaptation. Supporting this, Atlantic island populations of *R. bucephalophorus* show high genetic differentiation and high genetic distances among them (Talavera *et al.* 2010).

In conclusion, our greenhouse experiments revealed a high phenotypic plasticity for dispersal capacity in *R. bucephalophorus* that adds to growing evidence about the important role of phenotypic plasticity in dispersal traits of plants. In contrast, the production of SD versus LD diaspores is genetically determined, so that unlike dispersal capacity, dispersal distance is not plastic. Taking together habitats and sites, Atlantic islands and mainland coastal sands share high production of dispersible diaspores, high dispersal capacity and mid-dispersal strategy. In Atlantic islands, coastal sand populations were not represented at all, and so it is not possible to confound site and habitat effects. Atlantic islands and coastal sands differ in many aspects, but they share a climate without drastic differences between the seasons; this kind of habitat stability could select for the mid-dispersal strategy. Although most models dealing with the evolution of dispersal strategies assume that forces selecting for decreased dispersability also select for decreased dispersal distances (Murrell, Travis &



Dytham 2002; Bonte, Hovestadt & Poethke 2010), in *R. bucephalophorus* dispersal distance and dispersability showed contrasting patterns of variation. The fact that these two traits are differently determined could favour their different response to selective pressures.

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