The LINNEAN SOCIETY of London BOTANICAL Journal of the Linnean Society

Botanical Journal of the Linnean Society, 2014, **174**, 384–398. With 3 figures

Phylogenetic signal in growth and reproductive traits and in their plasticity: the *Descurainia* radiation in the Canary Islands

TOMÁŠ HERBEN[1,2]*, VĚRA RYDLOVÁ[1], TOMÁŠ FÉR[2], JAN SUDA[1,2], ZUZANA MÜNZBERGOVÁ[1,2], RADKA WILDOVÁ[1,3] and JAN WILD[1]

[1]*Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic*
[2]*Department of Botany, Faculty of Science, Charles University in Prague, Benátská 2, CZ-128 01 Praha 2, Czech Republic*
[3]*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48104, USA*

Received 1 October 2013; revised 5 November 2013; accepted for publication 13 November 2013

Despite the extensive use of phylogenetic methods in comparative plant biology, there is little information on how traits and their plastic responses can be affected by phylogenetic constraints (i.e. limitations in phenotypic expression resulting from the phylogenetic history of a lineage), particularly in plant radiations that may have occurred over a relatively short time period. In this study, we examined phylogenetic constraints in a monophyletic group of species of *Descurainia* (Brassicaceae) endemic to the Canary Islands. We measured growth and reproductive traits in a glasshouse experiment representing 17 populations of eight taxa previously analysed in a phylogenetic context. Two water availability treatments were used to assess the plasticity of the examined traits. Most of the traits did not show strong phylogenetic signal; only weak evidence for phylogenetic constraint was found in traits related to reproduction (total number of flowers, onset of flowering) and biomass allocation to roots. Substantial levels of plasticity were observed in all the examined traits, but plasticity showed little interaction between treatment and taxon, suggesting little divergence among taxa. Our study provides evidence that phylogenetic constraints in these quantitative traits, including their plastic expression, have not played a significant role in the pattern of phenotypic diversification of this island plant group. Phenotypic plasticity may thus have favoured adjustment to the habitats occupied by each species during the radiation process. *Botanical Journal of the Linnean Society*, 2014, **174**, 384–398.

ADDITIONAL KEYWORDS: Brassicaceae – conservatism – diversification – drought – genotype × environment interaction – phylogenetically independent contrasts.

INTRODUCTION

Life history theory has made remarkable advances in demonstrating the ways in which plant growth and reproductive traits can vary in response to the environment (Scheiner, 1993; van Tienderen, 1997; Tuljapurkar & Caswell, 1997; Silvertown, Dodd & Gowing, 2001), and these theoretical advances have been supported by empirical data from large sets of plant species (Silvertown *et al*., 1993; Grime *et al*., 1997; Menges, 2000). However, these relationships are subject to phylogenetic constraints, i.e. legacies of past evolutionary events on the current traits of the organism, including growth and reproductive traits, which are presumably closely related to its fitness ('phylogenetic effects' as defined by McKitrick 1993). Recent advances in molecular techniques and their use in phylogenetic reconstruction (Huelsenbeck *et al*., 2001) are providing the necessary tools to examine actual evolutionary histories of traits (see Harvey & Pagel, 1991; Schaal & Leverich, 2001; Kembel & Cahill, 2005), making it possible to identify

*Corresponding author. E-mail: herben@site.cas.cz

phylogenetically conserved components in plant traits. Such an approach has been used extensively for the analysis of morphological (Givnish, 1987; Böhle, Hilger & Martin, 1996; Dunbar-Co, Sporck & Sack, 2009) and ecological (Ackerly *et al*., 2000; Prinzing *et al*., 2001; Cornwell & Ackerly, 2009; Mayfield, Boni & Ackerly, 2009) traits, but only rarely for the explicit phylogenetic analysis of traits related to growth and reproduction (but see, for example, Verdu & Traveset, 2005; Muth & Pigliucci, 2006; Burns *et al*., 2010; Burns & Strauss, 2011).

A key component of plant fitness is the ability to respond to changing environments by plastic responses. Plasticity is essential in enabling a plant to survive in environments that vary over time or space (Scheiner, 1993; Sultan, 2000; Novoplansky, 2009). By enabling individuals to survive under a variety of conditions, it can help them to inhabit wider habitat ranges and may thus be a driver of population divergence and, presumably, speciation (Pigliucci, Murren & Schlichting, 2006; Ghalambor *et al*., 2007; Crispo, 2008). Differences in the levels of plasticity across a set of closely related taxa may indicate how this potential has been exploited during their evolution. Specifically, as plasticity is under genetic control (Schmitt, 1993; Pigliucci, Cammell & Schmitt, 1999), plasticity across taxa could also be subject to phylogenetic constraints. Yet, we know little about phylogenetic constraints involved in this process, and the existing findings are not consistent (Pigliucci *et al*., 1999; Kembel & Cahill, 2005). Strong phylogenetic constraints on plastic responses would indicate weak selection for plasticity, and thus data relating to this subject could help to resolve the evolutionary role of plasticity (van Kleunen & Fischer, 2005).

Phylogenetic constraints on traits related to growth and reproduction are best studied within groups of related species. Such species generally share growth form and other major life strategy features, permitting the identification of minor or incipient divergences (or their absence). This is a necessary condition for the degree of plasticity in these traits to be reliably assessed. Best examples of such groups are found in closely related taxa which originated during rapid radiation processes on oceanic archipelagos (Price & Wagner, 2004; Rundell & Price, 2009). Such radiations are a frequent evolutionary process on oceanic islands where geographical isolation has permitted only a few colonizing species to arrive from mainland source areas which underwent subsequent episodes of speciation (Givnish, Montgomery & Goldstein, 2004). Populations subjected to different selective regimes across environmental gradients may then accumulate genetic differences, ultimately leading to speciation. For example, evolutionary diversification in *Dubautia* Gaudich. (Asteraceae) of the Hawaiian silversword alliance has been accompanied by a significant degree of change at the physiological and morphological levels, including water relations (Robichaux, 1984), tissue elastic properties (Robichaux & Canfield, 1985) and plant architecture (Friar *et al*., 2006). Similarly, ecophysiological studies on Hawaiian lobelioids have shown that a common ancestor gave rise to a series of species differing in their ability to exploit light or water availability (Givnish *et al*., 2004; Montgomery & Givnish, 2008). In contrast with most morphological and physiological traits that often change during the course of lineage diversification, traits associated with reproductive output (including flowering phenology) usually remain stable and do not appear to undergo dramatic changes (Jorgensen & Olesen, 2001; Levin, 2006; García-Verdugo *et al*., 2014). However, not all evolutionary changes in insular radiations are adaptive, and random processes (e.g. genetic drift) can also promote evolution. A strong indication of the adaptive value of a trait is a parallel pattern of variation in phylogenetically distinct, but ecologically similar, species (Givnish, 1997). Because of strong pressure for the evolution of adaptive traits during the colonization of new habitats (Rundell & Price, 2009), insular radiations provide particularly good opportunities for distinguishing between evolutionarily conserved traits and those that change readily in evolution (Jorgensen & Olesen, 2001; García-Verdugo *et al*., 2014).

In this study, we examine phylogenetic constraints on traits relating to growth and reproduction and their plastic responses in a monophyletic group of closely related species. We combined data from a manipulative experiment with published phylogenetic data to examine phylogenetic constraints on a number of traits relating to growth and reproduction in species of *Descurainia* Webb & Berthel. (Brassicaceae) endemic to the Canary Islands. There are seven named *Descurainia* spp. in the Canary Islands (Arechavaleta *et al*., 2010), the phylogenetic relationships of which have been analysed previously (Goodson, Santos-Guerra & Jansen, 2006). First, we wish to identify those growth and reproductive traits that differ among closely related taxa within clades, and those that, in contrast, are stable within clades. Second, we seek to determine whether there is any phylogenetic constraint on the plasticity of these traits. The absence of such a signal would imply that plasticity has been changing in individual species freely (presumably in response to the heterogeneity in the environment), whereas conservatism in this trait would mean constraints on change in the capacity of the plastic response. We examine plastic responses to variation in the water regime, which is likely to be a key environmental driver in the studied group (see,

for example, Fernández-Palacios, 1992), and plants are known to show plastic responses to this factor (Aronson, Kigel & Shmida, 1993; Gianoli, Quezada & Suarez, 2009). Moreover, plastic responses to water availability have been demonstrated in several plant species and are known to vary across taxa and genotypes, showing genotype × environment (G × E) interactions (Sultan, 2001, 2009; Heschel *et al*., 2004; Rizhsky *et al*., 2004).

MATERIAL AND METHODS

Study region and study species

The Canary Islands comprise seven major islands with remarkable variation in elevation that are a part of the Macaronesian region. Recently, the Macaronesian flora has become the subject of intensive molecular phylogenetic and phylogeographical studies that have made clear that most of the endemic groups present are strictly monophyletic, i.e. each originated from a single colonization event (Silvertown, 2004; García-Verdugo *et al*., 2014). In addition, sharp ecological gradients between different ecological zones make Macaronesia an ideal region for studying evolution in response to environment.

Descurainia (Brassicaceae) comprises approximately 45 named species worldwide, with seven of them endemic to the Canary Islands (Bramwell, 1997; Goodson *et al*., 2006; Arechavaleta *et al*., 2010). These perennial species occur on four of the five high Canary Islands (La Palma, La Gomera, Tenerife and Gran Canaria), where they occupy a number of habitat types, including lowland scrub, pine forest and high-altitude desert ecological zones (Hohenester & Welss, 1993; Francisco-Ortega, Jansen & Santos-Guerra, 1996; Goodson *et al*., 2006). Among these taxa, *D. millefolia* Webb & Berthel. is the only widespread species, occurring in lowland scrub on Tenerife, La Gomera and La Palma. The island of Tenerife hosts three endemic species: *D. bourgeauana* Webb ex Christ (locally frequent in high-altitude desert habitats) and the rarer *D. gonzalesii* Svent. and *D. lemsii* Bramwell, both occurring in the upper pine forest zone. Two *Descurainia* spp. are endemic to Gran Canaria: the rare *D. artemisioides* Svent. in the western part of the island and *D. preauxiana* Webb ex Christ. in southern and central regions of the island. La Palma hosts one endemic species, *D. gilva* Svent., in the upper pine forest zone. There is also an uncertain report of *D. bourgeauana* on La Palma (discussed in Goodson *et al*., 2006). Phylogenetic reconstructions of *Descurainia* in the Canary Islands have been performed using the nuclear ribosomal internal transcribed spacers (ITSs) and seven non-coding plastid regions (Goodson *et al*., 2006). These results suggested that populations of *D. millefolia* on the island of Tenerife are differentiated from those populations sampled on the islands of La Palma and La Gomera, and are genetically closer to the other two taxa occurring on Tenerife (*D. gonzalesii* and *D. lemsii*).

Field collection

We searched for potential locations of *Descurainia* spp. using published literature sources and herbarium vouchers, and then visited the sites during a field trip in 2005. We sampled all named species, with the exception of *D. artemisioides*, which is endangered and is listed in the *Red Book of Vascular Plants of Spain* (Bañares *et al*., 2004). If a species was known to occur on several islands (*D. millefolia*), care was taken to ensure that samples were collected from each of them. Altogether, 17 populations of six named species on four islands (eight species/island combinations) were sampled (Table 1). Herbarium vouchers are kept in PRC.

For each population, we sought to collect seeds from at least 20 mother plants and kept seeds from each mother plant separately. However, owing to the limited number of fruiting plants during seed collection, progeny of only ten mother plants was collected from populations PC1, PC2, MT1 and MT2, and progeny of only two mother plants was collected from MP3. Seeds were kept in a dry place until the beginning of the experiment.

Phylogenetic approach

We calculated the relatedness of individual taxa using a published tree based on seven plastid regions (fig. 3 in Goodson *et al*., 2006). Distances along the tree branches, expressed as the sum of branch lengths from the first population to the second population via the closest connecting node, were taken as measures of the phylogenetic relatedness of the populations. As the populations used in the cited study and our populations were not necessarily the same, we lumped together all populations for each species on each island to correspond to the phylogenetic reconstruction of Goodson *et al*. (2006). Our approach is justified because the phylogenetic reconstruction was based on sequences of the ITS nuclear region and several plastid regions, which usually show limited variation at the intraspecific level. This yielded the following ten species/island units: *D. artemisioides*/Gran Canaria, *D. bourgeauana*/La Palma, *D. bourgeauana*/Tenerife, *D. gilva*/La Palma, *D. gonzalesii*/Tenerife, *D. lemsii*/Tenerife, *D. millefolia*/La Gomera, *D. millefolia*/La Palma, *D. millefolia*/Tenerife and *D. preauxiana*/Gran Canaria. Two of these (*D. artemisioides*/Gran Canaria and *D. bourgeauana*/La Palma) were not included in

Table 1. List of populations used in the study with their codes, identity, location information, habitat and herbarium voucher

Code	Taxon	Island	Coordinates	Elevation (m a.s.l.)	Habitat	Voucher no.
BT1	*Descurainia bourgeauana*	Tenerife	28°18′22.0″N, 16°33′29.5″W	2080	Sediments (pumice) and rocks of volcanic origin; sparse scrub vegetation [*Spartocytisus supranubius* (L.f) Christ ex G.Kunkel]	JS 2005-112
BT2	*D. bourgeauana*	Tenerife	28°16′03.3″N, 16°33′12.2″W	2070	Sediments (pumice) and rocks of volcanic origin; sparse scrub vegetation (*Spartocytisus supranubius*)	JS 2005-115
BT3	*D. bourgeauana*	Tenerife	28°13′14.1″N, 16°37′40.1″W	2130	Sediments and rocks of volcanic origin (pumice); sparse scrub vegetation (*Spartocytisus supranubius*)	JS 2005-101
GiP1	*D. gilva*	La Palma	28°46′41.0″N, 17°54′22.8″W	1700	Weathered rock; sparse grassland vegetation	JS 2005-145
GoT1	*D. gonzalesii*	Tenerife	28°15′54.1″N, 16°33′14.0″W	2070	Sediments (pumice) and rocks of volcanic origin; sparse scrub vegetation (*Spartocytisus supranubius*)	JS 2005-117
LT1	*D. lemsii*	Tenerife	28°21′48.7″N, 16°27′54.0″W	1970	Bare soil; pine forest ('Pinar')	JS 2005-124
MG1	*D. millefolia*	La Gomera	28°07′05.9″N, 17°19′38.1″W	825	Weathered rock; sparse vegetation dominated by *Erica arborea* L. ('Fayal-Brezal')	JS 2005-178
MP1	*D. millefolia*	La Palma	28°42′23.1″N, 17°56′50.0″W	540	Weathered rock; sparse vegetation dominated by *Erica arborea* ('Fayal-Brezal')	JS 2005-152
MP2	*D. millefolia*	La Palma	28°48′11.7″N, 17°57′54.3″W	300	Weathered rock; sparse herbaceous vegetation	JS 2005-153
MP3	*D. millefolia*	La Palma	28°40′48.6″N, 17°50′47.9″W	1020	Weathered rock in the valley of a temporary brook	JS 2005-160
MT1	*D. millefolia*	Tenerife	28°34′21.5″N, 16°09′24.5″W	540	Weathered rock; sparse vegetation dominated by *Erica arborea* ('Fayal-Brezal')	JS 2005-79
MT2	*D. millefolia*	Tenerife	28°34′23.0″N, 16°09′03.2″W	370	Weathered rock; sparse vegetation dominated by species of *Euphorbia* L. ('Tabaibal')	JS 2005-75
MT3	*D. millefolia*	Tenerife	28°33′21.1″N, 16°15′53.7″W	620	Weathered rock; sparse vegetation dominated by *Erica arborea* ('Fayal-Brezal')	JS 2005-74
MT4	*D. millefolia*	Tenerife	28°18′02.3″N, 16°50′30.4″W	205	Weathered rock	JS 2005-58
MT5	*D. millefolia*	Tenerife	28°21′43.4″N, 16°53′29.6″W	205	Weathered rock; sparse vegetation dominated by *Euphorbia* spp. ('Tabaibal')	JS 2005-62
PC1	*D. preauxiana*	Gran Canaria	28°03′44.0″N, 15°39′32.1″W	480	Weathered rock; sparse vegetation	JS 2005-212
PC2	*D. preauxiana*	Gran Canaria	27°59′28.4″N, 15°38′27.7″W	1340	Weathered rock; sparse vegetation	JS 2005-211

the experiment, but were included in the analysis of phylogenetic data. Goodson *et al*. (2006) showed *D. millefolia* to be paraphyletic, with the populations from different islands clustering more closely with other taxa than their purported conspecifics of different geographical origin. Thus, in our study, we have applied the label of 'taxon' to each of the ten above-listed units, and focused on the eight such taxa that we sampled. Average distances between pairs of these taxa were calculated as means of the pair phylogenetic distances between each of the sampled populations of a given taxon and each of the sampled populations of the other member of the pair in Goodson *et al*. (2006).

Experimental design and data collection

The cultivation experiment started in January 2006. Seeds were sterilized in a weak potassium permanganate solution and sown in small plastic containers in trays filled with potting soil and sand (2 : 1) in a glasshouse, and watered regularly. After 1 month, the seedlings were individually replanted into 3×3 cm^2 containers filled with potting soil and sand (1 : 1). After another month of growth, already established seedlings were planted into round containers of 17×17 cm^2 (*c*. 4 litres) in size with potting soil and sand (2 : 1) and watered daily. Twenty plants from each population were used; care was taken to use only one plant from each progeny of one mother plant for the experiment, whenever possible. The containers were kept in an unheated glasshouse on the premises of the Institute of Botany at Průhonice (50°00′N, 14°30′E) in the Czech Republic. After two further weeks of growth in the large containers, the plants were assigned to two treatments (i.e. ten replicate plants from each population in each treatment, the overall size of the experiment being 340 plants). If several plants from one mother plant were in cultivation, they were allocated to different treatments to minimize the number of half-siblings in each treatment. Plants in the high-water treatment were watered daily, whereas plants in the low-water treatment were watered approximately once every 5 days. The positions of plants in the experiment were shuffled approximately once every 3 weeks to avoid random effects of microenvironmental variation. Plant growth parameters were measured several times during the experiment (depending on the trait, see below). The parameters measured were plant height, number of leaves, number of branches and number of flowers. The experiment was terminated in January 2007, when plants were harvested, dried (at 60 °C) and weighed. The roots were washed to remove the substrate, dried and weighed. All but one plant survived until the end of the experiment.

Data analysis

Data from the growth experiment were processed to produce the following dependent variables for each individual: (1) plant height over the course of the experiment, after 68, 138 and 360 days (end of the experiment); (2) relative growth rate (RGR; see below); (3) number of branches and number of flowers at the end of the experiment; (4) onset of flowering; (5) biomass of individual plant parts at the end of the experiment; and (6) biomass allocation to individual plant parts at the end of the experiment. These variables are referred to as traits below.

Height-based RGR was calculated as $\frac{\log(h_2) - \log(h_1)}{t_2 - t_1}$, where h_2 and h_1 are the plant heights at the end and the beginning of the period over which RGR is calculated, respectively, and t_2 and t_1 are the last and first days of that period, respectively. RGR was calculated for two intervals: between the 52nd and 98th day of the experiment (early RGR) and between the 98th and 138th day of the experiment (late RGR). The early RGR captures the early growth phase and the first response to differential water availability in the low-water treatment, whereas the late RGR captures the speed at which the plants approach their final sizes. As flowering data were not collected on a daily basis, the date of onset of flowering was estimated assuming a linear rate of flower development as $t_0 = t_1 - \frac{f_1(t_2 - t_1)}{(f_2 - f_1)}$, where t_0 is the date to be estimated, t_1 and t_2 are two successive recording dates after flowering was recorded, and f_1 and f_2 are the numbers of flowers recorded at these dates. Plants that were alive but had not flowered when the experiment was terminated were, by convention, assigned an onset of flowering at the end of May 2007, assuming that these plants would flower in their second year. Biomass allocation was calculated as a proportion of the respective plant part (inflorescence, roots, stem with leaves, branches with leaves) out of the total plant biomass measured at the end of the experiment. These values were employed only in analyses that used aggregate data over populations or taxa. In statistical models of individual plants [general linear models (GLMs) below], allocation to a given plant part was analysed by taking the biomass of that part as a dependent variable and the total plant biomass as a covariate, instead of analysing allocations directly.

We used unrotated principal component analysis on a correlation matrix of trait values to summarize correlations among traits at the level of individual plants, to represent major trait syndromes (linear combinations of traits) and to separate variation in

shape from variation in size (for a discussion, see, for example, Somers, 1986). Biomass allocation variables were not included in this analysis because of their high correlation with absolute biomass values. Trait scores for individual plants were then analysed in the same manner as other dependent trait variables; they are denoted as Factor 1 and Factor 2 below [to distinguish them from the principal coordinate analysis (PCoA) axes that express phylogenetic relatedness between the taxa] and were used as independent variables in the analyses.

All dependent variables at the level of individual plants were analysed by means of GLMs using S-Plus ver. 2000 (MathSoft, 2000). Untransformed values of individual trait values were used because of their approximately normal distribution and homoscedasticity; reproduction-related variables (number of flowers, inflorescence biomass and inflorescence allocation) were square-root transformed before the analysis to improve homogeneity of variances. Two basic models were fitted to the data: (1) an ahistorical model with treatment, taxon and population (nested in taxon) as independent variables, and all meaningful interactions of these variables, to assess G × E interactions as a measure of variation in plasticity; and (2) a phylogenetic model. To fit a phylogenetic model assessing G × E interactions, we used the approach of Diniz-Filho, de Sant'Ana & Bini (1998) (see also Desdevises *et al*., 2003). We summarized the matrix of phylogenetic distances using non-standardized PCoA employing the function `dudi.pco` from the `ade4` package for R (Dray & Dufour, 2007); the analysis included the two taxa (*D. artemisioides*/Gran Canaria and *D. bourgeauana*/La Palma) that did not have corresponding plants in the experiment. Scores along the first two PCoA axes (first and second axes accounting for 65.4% and 20.8% of the total variation, respectively) were employed to capture phylogenetic relatedness of the eight taxa used in our experiment. The phylogenetic model was thus fitted to the experimental data with treatment, PCoA axis 1 score, PCoA axis 2 score, taxon (nested in PCoA axis 1 score and PCoA axis 2 score) and population (nested in taxon) as independent variables, and all meaningful interactions of these variables. *F*-tests were used to evaluate the significance of the individual terms of each of these models, accounting for the hierarchical structure of errors: taxon was thus used as the error level for PCoA axis 1 score and PCoA axis 2 score (phylogenetic model only) and population for taxon. Variance components of individual variables were calculated using the function `varcomp` in S-Plus 2000 (MathSoft, 2000) with restricted maximum likelihood as the estimation method, employing the same models as in the ahistorical GLM tests.

The phylogenetic signal of each trait mean and plasticity at the taxon level were further assessed using Pagel's λ (Freckleton, Harvey & Pagel, 2002). For this analysis, we used the mean and plasticity of each of the measured traits for each taxon, with plasticity defined as the difference in mean phenotypic values between treatments divided by the mean across treatments; plasticity in factor scores was defined as the factor score difference between treatments. Two tests were performed, testing the significance of the data under the hypothesis $\lambda = 0$ (no phylogenetic signal) and under the hypothesis $\lambda = 1$ (Brownian model of trait evolution over the phylogenetic tree, i.e. complete phylogenetic signal) using function `pgls` from the package `caper` for R (Orme, 2012). If neither of these tests was significant, we assumed that the power of the test was too low to draw any conclusion about the phylogenetic pattern in the trait. To account for interpopulation variation within taxa, identical analyses were performed at the population level with the means and plasticity of each trait defined as above. For the population-level analysis, we assumed that phylogenetic distances between populations within each taxon were equal to the mean within-taxon between-population distance from Goodson *et al*. (2006).

RESULTS

Analysis of phylogenetic distances

The first and second axes of the PCoA captured > 85% of the variation in the matrix phylogenetic distances among the ten taxon/island combinations. The first PCoA axis reflected the two deepest divisions of the tree obtained by Goodson *et al*. (2006), with *D. gilva* and *D. bourgeauana* on one side, *D. millefolia*/Tenerife and *D. lemsii*/Tenerife on the other side and *D. millefolia*/La Palma, *D. millefolia*/La Gomera, *D. gonzalesii* and both Gran Canaria species in the middle (Fig. 1). The second PCoA axis primarily separated Gran Canaria species (and *D. millefolia* on islands other than Tenerife) from the rest.

Growth experiment

Growth in height was rapid at the beginning of the experiment, but soon slowed down, with little height increase in the later phase of the experiment (from the fourth month of the experiment onwards; Fig. S1). Approximately 60% of the plants flowered. The effect of treatment was significant for most variables. However, there was no significant effect on the late RGR, number of branches and onset of flowering (Table 2).

The ahistorical GLM (Tables 2 and 3) showed that most of the variation in the examined traits was

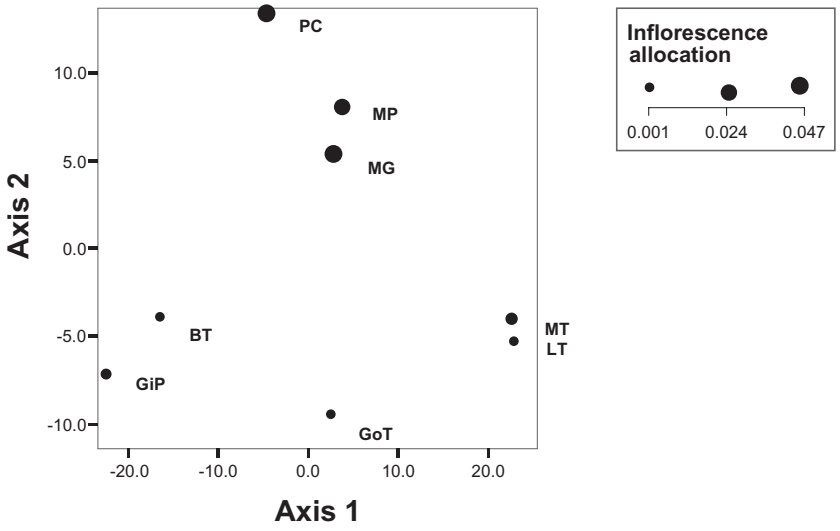

Figure 1. Example of a trait with phylogenetic signal. Points represent individual taxa plotted using the scores of principal coordinate analysis (PCoA) of phylogenetic relatedness; symbol sizes express the mean trait value for that taxon. Means over both environments are shown. BT, *Descurainia bourgeauana*/Tenerife; GiP, *D. gilva*/La Palma; GoT, *D. gonzalesii*/Tenerife; LT, *D. lemsii*/Tenerife; MG, *D. millefolia*/La Gomera; MP, *D. millefolia*/La Palma; MT, *D. millefolia*/Tenerife; PC, *D. preauxiana*/Gran Canaria. For the tests, see Table 4.

Table 2. Significance tests (*P* values) of individual terms of the ahistorical general linear model (GLM), with taxon, population, treatment and their interactions as the only explanatory variables. This model does not take into account phylogenetic relationships among taxa. Values significant at $\alpha = 0.05$ are in bold, values marginally significant at $\alpha = 0.1$ are in bold italics. Taxon×Trt, taxon × treatment interaction; Pop×Trt, population × treatment interaction. All variables, except heights and onset of flowering, were determined at the end of the experiment

	Treatment	Taxon	Taxon×Trt	Population (nested in taxon)	Pop×Trt (nested in Taxon×Trt)
D.f. effect	1	7	7	9	9
D.f. error	306	9	9	306	306
Total plant height after 68 days	**< 0.001**	0.447	0.427	**< 0.001**	***0.063***
Total plant height after 138 days	**< 0.001**	0.452	0.707	**< 0.001**	0.732
Total plant height after 360 days	**< 0.001**	0.268	**0.023**	**< 0.001**	0.921
Early relative growth rate	0.647	0.581	**0.034**	**< 0.001**	0.685
Late relative growth rate	0.230	**0.002**	0.180	0.261	0.248
Total number of flowers	**< 0.001**	**0.001**	0.691	**< 0.001**	0.339
Onset of flowering	0.487	**0.002**	0.256	**< 0.001**	0.227
Total number of branches	0.147	**< 0.001**	0.131	**0.028**	0.130
Total above-ground dry mass	**< 0.001**	***0.051***	***0.087***	**< 0.001**	0.281
Dry mass of all branches	**< 0.001**	**0.033**	0.117	**< 0.001**	0.148
Dry mass of inflorescences	**< 0.001**	**0.010**	**0.039**	**0.000**	0.974
Total root dry mass	**< 0.001**	**0.024**	**0.006**	**0.020**	0.598
Allocation to all branches	0.286	0.117	0.327	**< 0.001**	0.115
Inflorescence allocation	**0.015**	**0.029**	**0.064**	**< 0.001**	0.646
Root allocation	**0.010**	0.511	0.281	**< 0.001**	0.121
Factor 1 score	**< 0.001**	***0.084***	0.567	**< 0.001**	0.931
Factor 2 score	**< 0.001**	0.112	**0.033**	**< 0.001**	0.373

Table 3. Variance components for individual trait variables in the ahistorical general linear model (GLM). All variables, except height, growth rate and onset of flowering, were determined at the end of the experiment. Traits having variation caused by the 'taxon' factor larger than variation caused by the 'population' factor are indicated in bold

Variable	Taxon	Taxon × treatment	Population (nested in taxon)	Population × treatment (nested in taxon × treatment)	Residual
Total plant height after 68 days	0.000	0.013	0.372	0.040	0.575
Total plant height after 138 days	0.000	0.000	0.191	0.000	0.809
Total plant height after 360 days	0.000	**0.028**	0.244	0.000	0.728
Early relative growth rate	0.000	**0.048**	0.361	0.000	0.591
Late relative growth rate	0.233	**0.035**	0.000	0.026	0.705
Total number of flowers	**0.489**	0.001	0.043	0.029	0.437
Onset of flowering	**0.383**	0.018	0.056	0.021	0.522
Total number of branches	**0.383**	0.037	0.007	0.044	0.530
Total above-ground dry mass	**0.113**	**0.063**	0.097	0.011	0.716
Dry mass of all branches	**0.118**	**0.065**	0.069	0.035	0.714
Dry mass of inflorescences	**0.211**	**0.090**	0.130	0.000	0.570
Total root dry mass	0.048	**0.127**	0.048	0.000	0.777
Allocation to all branches	0.142	0.022	0.157	0.045	0.635
Inflorescence allocation	0.111	**0.162**	0.154	0.004	0.569
Root allocation	0.000	**0.044**	0.122	0.035	0.799
Factor 1 score	**0.146**	0.000	0.126	0.000	0.727
Factor 2 score	0.128	**0.103**	0.188	0.010	0.571

caused by the factors 'taxon' and 'population (nested in taxon)', with the relative proportions of contributions of these levels to variance differing depending on the variable examined. The taxa differed in growth-related traits (late RGR, above-ground biomass, branch biomass, root biomass) and in reproductive traits (onset of flowering, number of flowers and, marginally, allocation to flowering). When the taxon-related variation was removed, there was significant variation between individual populations in almost all traits. The effect of water availability treatments was also strong and affected many traits; plants from the low-water treatment were smaller (in height and above-ground biomass) and branched and flowered less than plants assigned to the high-water treatment (Table 2, Fig. S1). Several interactions between taxon and treatment were significant and numerically large (final plant height, early RGR, mass of inflorescences, total root mass), but none of the interactions between treatment and population was significant (Table 2, Fig. 2).

The phylogenetic GLM showed only weak phylogenetic signal in the structure of the examined traits (Table 4). There was a consistent phylogenetically related difference in inflorescence biomass and allocation and, to some extent, in above-ground biomass, root biomass and allocation (Table 4; see also Fig. 1). There was almost no phylogenetic signal in the plastic response to water availability (i.e. phylogeny × treatment interaction). The only exception was plasticity in plant size at the early phase of the experiment.

All traits measured in individual plants were strongly correlated (the first two principal component axes explained 50.9%). Factor 1 essentially captured the size variation of the plants (Fig. 3). Factor 1 thus separated sturdier plants that invest more in vegetative growth from plants that grow quickly, flower early and invest more in generative parts. GLM analysis showed that both factor scores were strongly related to treatment and population. Factor 1 had a marginally significant effect of 'taxon', although the amount of variation contributed by either 'taxon' or 'population' was low (Tables 2 and 4); it did not show any phylogenetic signal. Factor 2 had a significant effect of 'taxon × treatment' interaction (Tables 2 and 4), with a considerable proportion of variation caused by 'taxon' (and 'population'). Factor 2 also had a significant phylogenetic signal in the mean value over treatments and a marginally significant 'PCoA axes × treatment' interaction (Table 4).

Individual trait means at the taxon level did not show any significant difference from $\lambda = 0$, but showed a number of significant differences from $\lambda = 1$ (Table 5). This indicated that, at the taxon level, there was no strong phylogenetic signal in any of the study traits. For several traits, there was no significant difference from either $\lambda = 0$ or $\lambda = 1$, indicating that

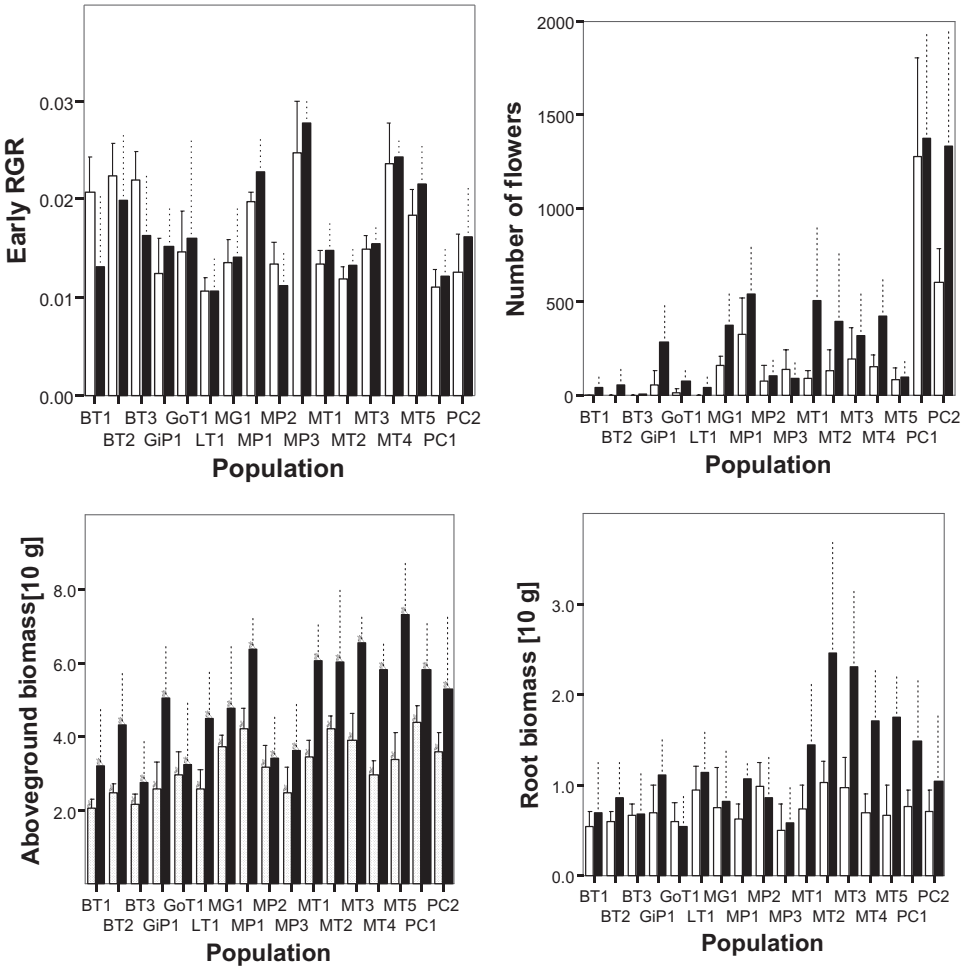

Figure 2. Changes of means of selected traits in response to treatments. Error bars indicate 95% confidence intervals. Open bars, dry treatment; filled bars, wet treatment. Multiple populations of the same taxon are designated by identical letters; for abbreviations of individual populations, see Table 1. BT, *Descurainia bourgeauana*/Tenerife; GiP, *D. gilva*/La Palma; GoT, *D. gonzalesii*/Tenerife; LT, *D. lemsii*/Tenerife; MG, *D. millefolia*/La Gomera; MP, *D. millefolia*/La Palma; MT, *D. millefolia*/Tenerife; PC, *D. preauxiana*/Gran Canaria. For the tests, see Table 2.

there was insufficient power to assess the validity of any phylogenetic hypothesis. At the population level, there were a few significant differences from $\lambda = 0$ (indicating phylogenetic signal); this was the case for flowering traits (number of inflorescences, inflorescence allocation, onset of flowering) and root traits (biomass allocation to roots). However, all traits showed significant differences from $\lambda = 1$ (Table 5), meaning that the patterns of trait variation among taxa were different from complete phylogenetic dependence, i.e. that expected under random (Brownian motion) evolution of the trait during the evolutionary history of the lineage.

Individual trait plasticities showed a similar pattern, with no significant differences from $\lambda = 0$ at the taxon level, and a few (again flowering and root biomass traits) at the population level. With one exception, all means and plasticities differed from $\lambda = 1$ at the population level. Significant phylogenetic signal in plasticity (i.e. significant difference from $\lambda = 0$) was shown by inflorescence number, biomass and allocation, and root biomass and allocation (Table 5). Evolution of inflorescence biomass was not distinguishable from the Brownian model (i.e. complete phylogenetic dependence).

DISCUSSION

Phylogenetic signal in individual traits

Using a monophyletic and ecologically divergent insular plant group, our study addressed the effect of phylogenetic relatedness on growth and reproductive traits and their plasticities. Most growth and

Table 4. Significance tests (*P* values) of individual terms of the phylogenetic general linear model (GLM), with the phylogenetic relationship [expressed as the first two principal coordinate analysis (PCoA) axes], taxon, population, treatment and their interactions as explanatory variables. Values significant at $\alpha = 0.05$ are in bold, values marginally significant at $\alpha = 0.1$ are in bold italics. AX12, main effect of both PCoA axes (phylogenetic effect on the trait mean); AX12×Trt, PCoA axes × treatment (phylogenetic effect on the trait plasticity); Taxon×Trt, taxon × treatment interaction; Pop×Trt, population × treatment interaction. All variables, except heights, growth rates and onset of flowering, were determined at the end of the experiment

	Treatment	AX12	AX12×Trt	Taxon	Taxon×Trt	Population (nested in taxon)	Pop×Trt (nested in Taxon×Trt)
D.f. effect	1	2	2	5	5	9	9
D.f. error	306	5	5	9	9	306	306
Total plant height after 68 days	**< 0.001**	0.383	**0.022**	0.456	0.875	**< 0.001**	***0.063***
Total plant height after 138 days	**< 0.001**	0.104	0.827	0.699	0.551	**< 0.001**	0.732
Total plant height after 360 days	**< 0.001**	0.179	0.213	0.431	***0.059***	**< 0.001**	0.921
Early relative growth rate	0.647	0.967	0.287	0.397	***0.061***	**< 0.001**	0.685
Late relative growth rate	0.230	0.653	0.210	**< 0.001**	0.301	0.261	0.248
Total number of flowers	**< 0.001**	***0.099***	0.699	**0.012**	0.565	**< 0.001**	0.339
Onset of flowering	0.487	0.157	0.324	**0.009**	0.266	**< 0.001**	0.227
Total number of branches	0.147	0.174	0.660	**< 0.001**	***0.098***	**0.028**	0.130
Total above-ground dry mass	**< 0.001**	0.101	0.309	0.204	0.129	**< 0.001**	0.281
Dry mass of all branches	**< 0.001**	0.105	0.322	0.149	0.161	**< 0.001**	0.148
Dry mass of inflorescences	**< 0.001**	**0.030**	0.904	0.106	**0.020**	**< 0.001**	0.974
Total root dry mass	**< 0.001**	***0.093***	0.268	0.134	**0.018**	**0.017**	0.598
Proportion of dry mass of all branches	0.286	0.863	0.458	***0.076***	0.254	**< 0.001**	0.115
Proportion of dry mass of inflorescences	**0.015**	**0.042**	0.429	0.262	**0.048**	**< 0.001**	0.646
Proportion of root dry mass	**0.010**	0.135	0.327	0.721	0.314	**< 0.001**	0.121
Factor 1 score	**< 0.001**	0.191	0.929	0.181	0.411	**< 0.001**	0.931
Factor 2 score	**< 0.001**	**0.047**	0.146	0.435	***0.098***	**< 0.001**	0.373

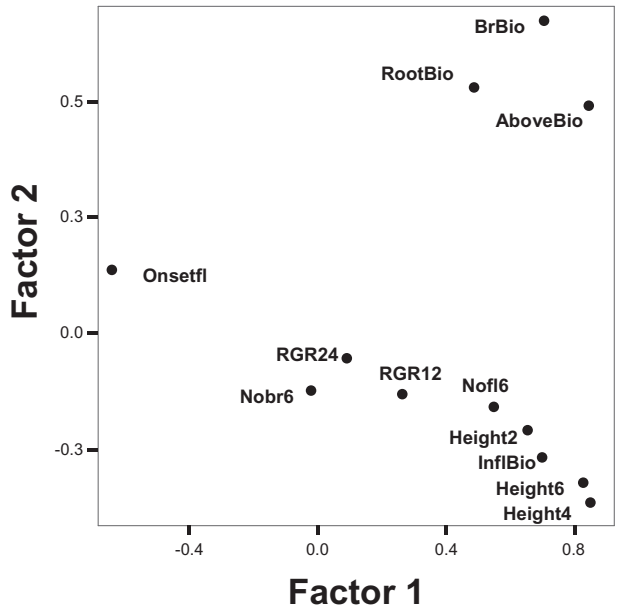

Figure 3. Principal component analysis of the traits: loadings of individual variables. The first axis explains 39.2% and the second axis 11.7% of the total variation. Trait abbreviations: Height2, total plant height on the 98th day; Height4, total plant height on the 138th day; Height6, total plant height at the end of the experiment; RGR12, early relative growth rate; RGR24, late relative growth rate; Onsetfl, onset of flowering; Nobr6, total number of branches; Nofl6, total number of flowers; AboveBio, total above-ground dry mass; BrBio, dry mass of all branches; InflBio, dry mass of inflorescences; RootBio, total root dry mass. Unless otherwise stated, all size and allocation variables are measured at the end of the experiment.

allocation traits exhibited significant variation in their means among population and taxa. In general, growth-related traits (such as plant height) were rather population specific with low variation among taxa; in contrast, flowering and allocation traits typically had large and significant amounts of variation residing at the taxon level and wide variation among taxa.

Despite wide phenotypic variation among taxa, all analyses showed that phylogenetic signal in these traits was rather weak or undetectable. There was weak evidence of phylogenetic conservatism in traits related to reproductive output (number of flowers, allocation to inflorescences) and biomass allocation to roots. Flowering traits are known to be conservative in many different groups (Wright & Calderon, 1995; Chazdon *et al*., 2003; Griffiths & Lawes, 2006). Although we cannot identify with certainty the key selective processes that took place during the evolution of this group, it is likely that the colonization of new habitats (e.g. lowland scrub, alpine zone or pine forests) must have been linked to selection on traits associated with adaptation to different water regimes.

Trait plasticity

In contrast with substantial taxon-level variation in trait means, variation in plastic responses among taxa was much lower, and differences between populations were even lower, with no significant population × treatment interactions at the population level (Tables 2 and 3). Low taxon-level and population-level differences in plasticity were found despite the fact that the mean plastic response (i.e. main effect of the treatment) was strong in many examined traits. Plasticity in most traits showed weak or a lack of phylogenetic signal; traits that showed conserved variation in plasticity were often those that also showed conserved variation in the means (such as total number of flowers or total root mass; Table 5). The sparse data available from other plant groups show no phylogenetic signal in growth traits (in response to light; Pigliucci *et al*., 1999), but phylogenetic constraints on plasticity in root allocation (Kembel & Cahill, 2005).

Low variation in trait plasticity among taxa and populations has two possible explanations: (1) there has been no differential selection on trait plasticity between the habitats of individual species because the habitats of all species are similar; or (2) habitats are different, but plastic responses to different water availability are strongly phylogenetically conserved in the whole clade and do not respond at all to existing selection (possibly also a result of the prevalence of passive over active plasticity; van Kleunen & Fischer, 2005). Available evidence for water regimes of habitats shows that: (1) drought is universal in the habitats of all *Descurainia* spp.; and (2) it typically has an important temporal component throughout the season which may differ among habitats (Fernández-Palacios, 1992). Published studies of drought-related plasticity have shown extensive interactive effects of treatment and source population or genotype on plasticity when populations coming from habitats differing in water regime are compared (Sultan & Bazzaz, 1993; Heschel *et al*., 2004). This may indicate that plasticity in drought-related traits need not be strongly conserved and that similarity across all taxa could indeed be caused by similarity in their habitats (see also Niinements & Valladares, 2006). This is further supported by the fact that most traits that showed interaction between taxon and treatment did not show a significant phylogenetic component in their variation (such as total plant height or early RGR).

Table 5. Significance tests (P values wherever < 0.1) of $\lambda = 0$ and $\lambda = 1$ at the taxon and population levels. All variables, except height, growth rate and onset of flowering, were determined at the end of the experiment. Cases with insufficient power to assess any phylogenetic hypothesis [i.e. when tests of both $\lambda = 0$ and $\lambda = 1$ are non-significant (n.s.)] are indicated in italics

Level	Taxon				Population			
Variable tested	Mean		Plasticity		Mean		Plasticity	
Hypothesis	$\lambda = 0$	$\lambda = 1$	$\lambda = 0$	$\lambda = 1$	$\lambda = 0$	$\lambda = 1$	$\lambda = 0$	$\lambda = 1$
Total plant height after 68 days	*n.s.*	*n.s.*	n.s.	0.0673	n.s.	0	n.s.	0
Total plant height after 138 days	*n.s.*	*n.s.*	n.s.	0.0025	n.s.	0	n.s.	0
Total plant height after 360 days	n.s.	0.0404	n.s.	0.0151	n.s.	0	n.s.	0.0056
Early relative growth rate	n.s.	0.0318	n.s.	0.0027	n.s.	0	n.s.	0
Late relative growth rate	n.s.	0.0388	*n.s.*	*n.s.*	n.s.	0.0036	n.s.	0
Total number of flowers	*n.s.*	*n.s.*	*n.s.*	*n.s.*	0.0011	0.0007	0.0143	0
Onset of flowering	n.s.	0.0902	n.s.	0.0572	0.039	0.0007	n.s.	0
Total number of branches	n.s.	0.004	n.s.	0.006	0.0063	0.0078	n.s.	0
Total above-ground dry mass	n.s.	0.0483	n.s.	0.0062	n.s.	0	n.s.	0
Dry mass of all branches	n.s.	0.0063	n.s.	0.0224	n.s.	0	n.s.	0
Dry mass of inflorescences	*n.s.*	*n.s.*	*n.s.*	*n.s.*	n.s.	0	0	0.005
Total root dry mass	n.s.	0.009	n.s.	0.0411	0.0433	0	0.0549	0
Proportion of dry mass of all branches	n.s.	0.0048	n.s.	0.0094	n.s.	0	n.s.	0
Proportion of dry mass of inflorescences	*n.s.*	*n.s.*	*n.s.*	*n.s.*	0.0709	0	0	n.s.
Proportion of root dry mass	n.s.	0.008	n.s.	0.031	n.s.	0	0.084	0
Factor 1 scores	n.s.	0.081	n.s.	0.0133	n.s.	0	n.s.	0
Factor 2 scores	n.s.	0.0052	n.s.	0.0046	n.s.	0	n.s.	0

Limitations of the study

The power of the experiment to detect significant within-taxon variation in means and plasticities was constrained by the fact that some rare taxa (*D. gilva*, *D. gonzalesii* and *D. lemsii*) were each represented by only one population in the experiment. This means that the amount of variation among populations was estimated using only the most common species (namely *D. bourgeauana*, *D. millefolia* from Tenerife and *D. millefolia* from La Palma). However, examination of the pattern of variation in the examined traits across these taxa showed no major interspecific differences, suggesting that this is likely to be true for the clade as a whole.

The low number of taxa in the whole group also makes the identification of phylogenetic signals difficult (see Freckleton *et al*., 2002), and this was the likely reason for the inconclusive results obtained at the taxon level, where we did not find evidence of phylogenetic constraints for most traits because of a lack of power (Table 5). For these traits, the dataset is not sufficiently informative concerning their phylogenetic dependence. Our population-level analysis using 17 data points was more powerful to detect significant differences (Freckleton *et al*., 2002), and results from these analyses are more robust. The tests were typically sufficiently powerful to reject one of the extreme phylogenetic hypotheses (absence of any phylogenetic signal vs. trait evolution determined by phylogenetic dependence), but estimates of λ were still wide, leaving considerable uncertainty about the actual degree of phylogenetic dependence.

In addition, results on plastic responses are affected by the choice of treatment used in this study. The interpretation of plastic responses from the experiment was based on the assumption that responses in the glasshouse experiment approximate well to plant behaviour in the field. The results showed that differences between treatments were strong, and plants in the low-water treatment clearly performed considerably more poorly, indicating that the levels used were meaningful. However, the glasshouse regime is different from that in the field, and thus plastic responses may represent a different portion of the reaction norm of the species than that displayed by plants under natural conditions. Given the strong response of our plants to the experimental treatments, however, it is reasonable to assume that the sampled part of the reaction norm bears relevant information concerning the expression of plasticity in the study group.

The interpretation of trait plasticity should take into account the fact that response to the low-water regime is a combined effect of the behavioural response of the plant to low water as a stimulus (by

altering its developmental programme, for example) and of simple differences in productivity between the treatments differing in water availability (i.e. active and passive plasticity, respectively; van Kleunen & Fischer, 2005). Multivariate analysis can help to separate these components of plasticity: plasticity in the second axis captures shape-related variation independent of size, which is likely to be caused by a behavioural response.

Another issue is the high level of residual variation observed for many traits (Table 3). This can be partially explained by genetic differences among individuals experiencing different levels of treatment. It should be noted that genetically different individuals, not clones, were used in each treatment, which introduces some bias for the estimation of plasticity. Maternal effects may also account for these results as, in most cases, each plant was a descendent of a different field-occurring mother plant. Despite these limitations, we identified a number of significant relationships indicating sufficient power to reject the null hypothesis in some cases.

CONCLUSIONS

Our study detected high levels of phenotypic variation in growth and reproductive traits among individual *Descurainia* spp., but the analyses did not support strong phylogenetic patterns for these traits across the studied taxa. Weak phylogenetic signals were found in some reproductive traits (inflorescence biomass and allocation) and biomass allocation to roots, but most traits appear to have been labile over the course of the radiation. These results suggest the prevalence of putatively adaptive responses over constraints as a result of common ancestry. Levels of plasticity in all the examined traits were similar across taxa. Trait plasticity was even less phylogenetically constrained than trait mean values, which probably favoured the colonization of habitats during the evolution of this lineage.

ACKNOWLEDGEMENTS

We thank the Administration of the Parque Nacional de Las Cañadas del Teide and the Parque Nacional de Garajonay for permits. Karin Kottová helped us with the garden experiment. We thank Jonathan Rosenthal for comments and corrections of an earlier draft of this text, and the editor and two anonymous referees for their thorough reading and helpful comments. The research was supported by the Czech Science Foundation (grants 206/04/0081 and P505/12/1007), Academy of Science of the Czech Republic (long-term research development project no. RVO 67985939) and the Ministry of Education, Youth and Sports of the Czech Republic (institutional resources for the support of research).

REFERENCES

Ackerly DD, Dudley SA, Sultan SE, Schmitt J, Coleman JS, Linder CR, Sandquist DR, Geber MA, Evans AS, Dawson TE, Lechowicz MJ. 2000. The evolution of plant ecophysiological traits: recent advances and future directions. *Bioscience* **50:** 979–995.

Arechavaleta M, Rodríguez S, Zurita N, García A, eds. 2010. *Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. 2009*. Las Palmas: Gobierno de Canarias.

Aronson J, Kigel J, Shmida A. 1993. Reproductive allocation strategies in desert and Mediterranean populations of annual plants grown with and without water-stress. *Oecologica* **93:** 336–342.

Bañares Á, Blanca G, Güemes J, Moreno JC, Ortiz S, eds. 2004. *Atlas y Libro Rojo de la flora vascular amenazada de España*. Madrid: Dirección General de Conservación de la Naturaleza.

Böhle UR, Hilger HH, Martin WF. 1996. Island colonization and evolution of the insular woody habit in *Echium* L. (Boraginaceae). *Proceedings of the National Academy of Sciences of the United States of America* **93:** 11 740–11 745.

Bramwell D. 1977. A revision of *Descurainia* Webb. & Berth. section *Sisymbriodendron* (Christ) O. E. Schulz in the Canary Islands. *Botanica Macaronesica* **4:** 31–53.

Burns JH, Blomberg SP, Crone EE, Ehrlén J, Knight TM, Pichancourt J-B, Ramula S, Wardle GM, Buckley YM. 2010. Empirical tests of life-history evolution theory using phylogenetic analysis of plant demography. *Journal of Ecology* **98:** 334–344.

Burns JH, Strauss SY. 2011. More closely related species are more ecologically similar in an experimental test. *Proceedings of the National Academy of Sciences of the United States of America* **108:** 5302–5307.

Chazdon RL, Careaga S, Webb C, Vargas O. 2003. Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecological Monographs* **73:** 331–348.

Cornwell WK, Ackerly DD. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* **79:** 109–126.

Crispo E. 2008. Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation and gene flow. *Journal of Evolutionary Biology* **21:** 1460–1469.

Desdevises Y, Legendre P, Azouzi L, Morand S. 2003. Quantifying phylogenetically structured environmental variation. *Evolution* **57:** 2647–2652.

Diniz-Filho JAF, de Sant'Ana CER, Bini LM. 1998. An eigenvector method for estimating phylogenetic inertia. *Evolution* **52:** 1247–1262.

Dray S, Dufour AB. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* **22:** 1–20.

Dunbar-Co S, Sporck MJ, Sack L. 2009. Leaf trait diversification and design in seven rare taxa of the Hawaiian *Plantago* radiation. *International Journal of Plant Sciences* **170:** 61–75.

Fernández-Palacios JM. 1992. Climatic responses of plant species on Tenerife, the Canary Islands. *Journal of Vegetation Science* **3:** 595–602.

Francisco-Ortega J, Jansen RK, Santos-Guerra A. 1996. Chloroplast DNA evidence of colonization, adaptive radiation, and hybridization in the evolution of the Macaronesian flora. *Proceedings of the National Academy of Sciences of the United States of America* **93:** 4085–4090.

Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist* **160:** 712–726.

Friar EA, Prince LM, Roalson EH, McGlaughlin ME, Cruse-Sanders JM, De Groot SJ, Porter JM. 2006. Ecological speciation in the East Maui-endemic *Dubautia* (Asteraceae) species. *Evolution* **60:** 1777–1792.

García-Verdugo C, Baldwin BG, Fay MF, Caujapé-Castells J. 2014. Life history traits and patterns of diversification in oceanic archipelagos: a metaanalysis. *Botanical Journal of the Linnean Society* **174:** 334–348.

Ghalambor CK, McKay JK, Carroll SP, Reznick DN. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology* **21:** 394–407.

Gianoli E, Quezada IM, Suarez LH. 2009. Leaf damage decreases fitness and constrains phenotypic plasticity to drought of a perennial herb. *Acta Oecologica-International Journal of Ecology* **35:** 752–757.

Givnish TJ. 1987. Comparative studies of leaf form – assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist* **106** (Suppl.): 131–160.

Givnish TJ. 1997. Adaptive radiation and molecular systematics: issues and approaches. In: Givnish TJ, Sytsma KJ, eds. *Molecular evolution and adaptive radiation*. London: Oxford University Press, 1–54.

Givnish TJ, Montgomery RA, Goldstein G. 2004. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. *American Journal of Botany* **91:** 228–246.

Goodson BE, Santos-Guerra A, Jansen RK. 2006. Molecular systematics of *Descurainia* (Brassicaceae) in the Canary Islands: biogeographic and taxonomic implications. *Taxon* **55:** 671–682.

Griffiths ME, Lawes MJ. 2006. Biogeographic, environmental, and phylogenetic influences on reproductive traits in subtropical forest trees, South Africa. *Ecography* **29:** 614–622.

Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hand DW, Hannah MA, Hillier SH, Hodkinson DJ, Jalili A, Liu Z, Mackey JML, Matthews M, Mowforth MA, Neal AM, Reader RJ, Reiling K, Ross-Fraser W, Spencer RE, Sutton F, Tasker DE, Thorpe PC, Whitehouse J. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* **79:** 259–281.

Harvey PH, Pagel MD. 1991. *The comparative method in evolutionary biology*. Oxford: Oxford Series in Ecology and Evolution, Oxford University Press.

Heschel MS, Stinchcombe JR, Holsinger KE, Schmitt J. 2004. Natural selection on light response curve parameters in the herbaceous annual, *Impatiens capensis*. *Oecologia* **139:** 487–494.

Hohenester A, Welss W. 1993. *Exkursionsflora für die Kanarische Inseln*. Stuttgart: Eugen Ulmer.

Huelsenbeck JP, Ronquist F, Nielsen R, Bollback JP. 2001. Evolution – Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* **294:** 2310–2314.

Jorgensen TH, Olesen JM. 2001. Adaptive radiation of island plants: evidence from *Aeonium* (Crassulaceae) of the Canary Islands. *Perspectives in Plant Ecology, Evolution and Systematics* **4:** 29–42.

Kembel SW, Cahill JF. 2005. Plant phenotypic plasticity belowground: a phylogenetic perspective on root foraging trade-offs. *American Naturalist* **166:** 216–230.

van Kleunen M, Fischer M. 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist* **166:** 49–60.

Levin DA. 2006. Flowering phenology in relation to adaptive radiation. *Systematic Botany* **31:** 239–246.

MathSoft. 2000. *S-PLUS 2000*. Seattle, WA: MathSoft.

Mayfield MM, Boni MF, Ackerly DD. 2009. Traits, habitats, and clades: identifying traits of potential importance to environmental filtering. *American Naturalist* **174:** E1–E22.

McKitrick MC. 1993. Phylogenetic constraint in evolutionary theory: has it any explanatory power? *Annual Reviews of Ecology and Systematics* **24:** 307–330.

Menges ES. 2000. Population viability analyses in plants: challenges and opportunities. *Trends in Ecology and Evolution* **15:** 51–56.

Montgomery RA, Givnish TJ. 2008. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: dynamic photosynthetic responses. *Oecologia* **155:** 455–467.

Muth NZ, Pigliucci M. 2006. Traits of invasives reconsidered: phenotypic comparisons of introduced invasive and introduced noninvasive plant species within two closely related clades. *American Journal of Botany* **93:** 188–196.

Niinements U, Valladares F. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs* **76:** 521–547.

Novoplansky A. 2009. Picking battles wisely: plant behaviour under competition. *Plant Cell Environment* **32:** 726–741.

Orme D. 2012. *The caper package: comparative analysis of phylogenetics and evolution in R*. Vienna: R Foundation for Statistical Computing.

Pigliucci M, Cammell K, Schmitt J. 1999. Evolution of phenotypic plasticity: a comparative approach in the phylo-

genetic neighbourhood of *Arabidopsis thaliana*. *Journal of Evolutionary Biology* **12:** 779–791.

Pigliucci M, Murren CJ, Schlichting CD. 2006. Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology* **209:** 2362–2367.

Price JP, Wagner WL. 2004. Speciation in Hawaiian angiosperm lineages: cause, consequence, and mode. *Evolution* **58:** 2185–2200.

Prinzing A, Durka W, Klotz S, Brandl R. 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society of London B* **268:** 2383–2389.

Rizhsky L, Liang HJ, Shuman J, Shulaev V, Davletova S, Mittler R. 2004. When defense pathways collide. The response of *Arabidopsis* to a combination of drought and heat stress. *Plant Physiology* **134:** 1683–1696.

Robichaux RH. 1984. Variation in the tissue water relations of two sympatric Hawaiian *Dubautia* species and their natural hybrid. *Oecologia* **65:** 75–81.

Robichaux RH, Canfield JE. 1985. Tissue elastic properties of eight Hawaiian *Dubautia* species that differ in habitat and diploid chromosome number. *Evolution* **66:** 77–80.

Rundell RJ, Price TD. 2009. Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in Ecology and Evolution* **24:** 394–399.

Schaal BA, Leverich WJ. 2001. Plant population biology and systematics. *Taxon* **50:** 679–695.

Scheiner SM. 1993. Genetics and evolution of phenotypic plasticity. *Annual Reviews of Ecology, Evolution, and Systematics* **24:** 35–68.

Schmitt J. 1993. Reaction norms of morphological and life-history traits to light availability in *Impatiens capensis*. *Evolution* **47:** 1654–1668.

Silvertown J. 2004. The ghost of competition past in the phylogeny of island endemic plants. *Journal of Ecology* **92:** 168–173.

Silvertown J, Dodd M, Gowing D. 2001. Phylogeny and the niche structure of meadow plant communities. *Journal of Ecology* **89:** 428–435.

Silvertown J, Franco M, Pisanty I, Mendoza A. 1993. Comparative plant demography – relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* **81:** 465–476.

Somers KM. 1986. Multivariate allometry and removal of size with principal component analysis. *Systematic Zoology* **35:** 359–368.

Sultan SE. 2000. Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science* **5:** 537–542.

Sultan SE. 2001. Phenotypic plasticity for fitness components in *Polygonum* species of contrasting ecological breadth. *Ecology* **82:** 328–343.

Sultan SE. 2009. Darwinism renewed: contemporary studies of plant adaptation. *New Phytologist* **183:** 497–501.

Sultan SE, Bazzaz FA. 1993. Phenotypic plasticity in *Polygonum persicaria*. II. Norms of reaction to soil moisture and the maintenance of genetic diversity. *Evolution* **47:** 1032–1049.

Tuljapurkar S, Caswell H. 1997. *Structured-population models in marine, terrestrial, and freshwater systems*. New York: Chapman and Hall.

van Tienderen PH. 1997. Generalists, specialists and the evolution of phenotypic plasticity in sympatric populations of distinct species. *Evolution* **51:** 1372–1380.

Verdu M, Traveset A. 2005. Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. *Ecology* **86:** 1385–1394.

Wright SJ, Calderon O. 1995. Phylogenetic patterns among tropical flowering phenologies. *Journal of Ecology* **83:** 937–948.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Plant growth in height over the course of the experiment.