

Changes in resource-use strategy and phenotypic plasticity associated with selection for yield in wild species native to arid environments



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ARTICLE INFO

Article history:

Received 21 May 2014

Received in revised form

14 July 2014

Accepted 11 September 2014

Available online

Keywords:

Selection

Acquisitive

Conservative

Reproductive effort

Trade-offs

ABSTRACT

Along history, wild plants have been introduced into cultivation and domestic derivatives radically altered by this move due to changes in selection pressure: wild species are exposed to natural selection that operates to continue survival and domesticated species to artificial selection that emphasized yield. Here we assess whether selection for yield triggered a shift in resource-use strategy and changes in phenotypic plasticity. We compared co-generic wild and domesticated species grown in a common garden under two levels of water availabilities. Our results indicate that resource-use strategy shifted from conservative to acquisitive. The change in selection force from survival to reproduction provoked an increase in mean values of reproduction-related traits and a decrease in survival-related traits. Trade-offs between reproduction and storage were found in both groups. This occurred concurrently with an increase in phenotypic plasticity of most traits. Wild species showed higher homeostasis than domesticated species. Despite the lesser homeostasis of the latter, improvements in reproductive traits were not completely reversible under low resource availability: across environments domesticated species always showed higher reproductive biomass and reproductive effort than their wild relatives. The combination of higher mean values of advantageous traits and greater plasticity might contribute to the success of domesticated species in plentiful environments.

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1. Introduction

Along history, thousands of wild plant species have been introduced into cultivation and, in the majority of these cases the domestic derivatives are radically altered by this move (Zohary, 2001). Agricultural environments often present strong ecological contrasts with the environments in which the wild relatives of crop plants grow (Denison et al., 2003). Therefore, alterations in vegetation phenology, growth and reproductive traits occur (Matesanz et al., 2010) essentially because plants are subjected to different levels of stress and distinctive selection pressures. Wild species, specially those from arid lands, are exposed to natural selection that operates to continue survival under abiotic and biotic stress while domesticated species are subjected to artificial selection that emphasizes yield in the resource-richest habitats. Criteria for fitness are expected to change dramatically under both regimes (Jackson and Koch, 1997). In resource-poor environments, wild plant fitness is maximized by effectively conserving and protecting acquired resources (i.e. low relative growth-rate, low specific leaf

area (SLA), high leaf longevity and antioxidant enzymes activity; high allocation to roots and reserves; Chapin et al., 1993; Catorci et al., 2012; García-Palacios et al., 2013; Zhou et al., 2014) while in plentiful environments domesticated plants are better at exploiting available resources (i.e. high growth rate, high SLA and low allocation to roots and reserves; Pérez-Ramos et al., 2013). Consequently, the environmental changes associated with domestication should favor resource-acquisition strategies, compared with resource-conservation strategies of wild relatives. Despite such a shift in strategy appears to be one of the dominant themes of the evolutionary ecology of domestication (McKey et al., 2012), there are few experimental works comparing resource-use strategy and changes in allocation patterns between wild species and domesticated derivatives.

Thousands of agronomic works dealing with domestication focus on crucial domestication traits of cereals and grain legumes (see Zohary, 2001; Meyer et al., 2012; Abbo et al., 2014, for reviews on domestication). Providing that most of successful crop improvement programs to enhance crop yields have been performed under non-limiting conditions, barely a handful of agronomic literature refers to domestication in water-scarce environments (i.e. Richards, 2006; Cattivelli et al., 2008; Dierig

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et al., 2011; Hall and Richards, 2012) and even fewer emphasizes the development of trade-offs (i.e. Rosenthal and Dirzo, 1997; Massey and Hartley, 2000; García-Palacios et al., 2013) or shifts from a resource conservation strategy to a resource acquisition strategy provoked by domestication (Mondolot et al., 2008; McKey et al., 2012; Ménard et al., 2013).

Additionally, little is known about the sources of trait variation associated to modifications in resource-use strategy. Presumably, plants with differences in allocation strategies are characterized not only in mean differences, but also in the plasticity of traits (Nicotra et al., 2010). Literature suggests that plasticity may have changed substantially during the process of domestication and that exploitative species such as domesticated plants are more phenotypically variable and express more phenotypic plasticity than conservative species (i.e. Grime, 1979; Chapin, 1980). But given that plasticity is specific for a character in relation to a particular environmental factor (Bradshaw, 1965), reports of increased or decreased plasticity of certain traits coexist without prejudice (i.e. Calderini and Slafer, 1999; Sadras, 2007; McKey et al., 2012; Ménard et al., 2013). Nonetheless, most works are focus on plasticity of yield, yield components and phenological development (i.e. Sadras et al., 2009; Peltonen-Sainio, 1990; Sadras and Slafer, 2011) and it is still doubtful whether selection had led to increased or decreased plasticity in traits indirectly associated with yield (Nicotra et al., 2010). Additionally, a large body of controversial literature exists on the influence of the environment on plasticity. Alpert and Simms (2002) sustain that human selection, performed in uniform high nutrient is expected to promote genetic differentiation rather than plasticity, because when the plant perceives the environment as uniform there will be no advantage to plasticity. Likewise, plasticity should be also limited in consistently stressful environments because plastic responses are more costly when resources are limited (Valladares et al., 2006). Unpredictable environments, on the other hand, can lead to increased phenotypic plasticity (Denison et al., 2003) because plastic responses that allow individuals to track and manifest the optimal phenotype can increase individual fitness (Tonsor et al., 2013).

Here, we aimed to assess whether selection for high-yield in a plentiful and relatively uniform environment had led to shifts in resource-use strategy and changes in the phenotypic plasticity of traits associated with fitness and with plant adjustment to water availability. We assumed that selection increased mean seed yield, as this trait is the main target of selection (Marshall, 1991), but we also searched for indirect changes in traits related to growth and survival, triggered during the process of domestication. Specifically we ask:

- (1) Did selection entail a shift in resource-use strategy, from conservative to acquisitive?
- (2) Which traits are correlated to the target traits of selection and therefore indirectly modified by selection?
- (3) Does selection change the association between traits related to survival and reproduction?
- (4) Has selection led to changes in traits plasticity in response to water availability? (i.e. Are domesticated species more or less plastic than their co-generic wild species?)

In order to answer to those questions, we compared wild and domesticated species of rosette plants, the first group composed by wild species of *Physaria* (Nuttall ex Torrey & A. Gray) A. Gray (Brassicaceae) and *Oenothera* L. (Onagraceae) native to low-resource environments and the second one by a set of domesticated co-generic species bred for high-yield under non-limiting conditions. The comparison of domesticated plants and their wild relatives expands the understanding of evolution and adaptation to

the environment when plants of similar genetic backgrounds are subject to differences in selection pressures (Jackson and Koch, 1997). In this regard, selection for increased yield provides a unique opportunity to explore the evolution of resource acquisition strategies and phenotypic plasticity (Pujol et al., 2008). We considered wild and domesticated species as emergent groups (*sensu* Lavorel et al., 1997). Both groups were cultivated in a common garden under two regimes of water availability. Traits correlated with fitness and traits associated to plant adjustment to the environment were evaluated. The three components of plant fitness (growth, reproduction and survival) could be assessed by the measure of plant biomass, reproductive output and plant survival (Violle et al., 2007). Here, we used total biomass as fitness proxy for growth (Couso and Fernández, 2012), reproductive biomass and reproductive effort as fitness proxies for reproduction (Violle et al., 2007; Nicotra and Davidson, 2010) and allocation to carbohydrates reserves as fitness proxy for survival (Kobe, 1997; Vilela et al., 2008). We described the association between traits because it is not clear how the co-variations between them and their plasticity determine variations in species productivity (Pontes et al., 2010).

2. Materials and methods

2.1. Plant materials

We chose as experimental system herbs of *Physaria* (Brassicaceae) and *Oenothera* (Onagraceae) native to semi-arid and arid areas of America (Rollins and Shaw, 1973; Hoch, 1988). These genera exist as an acaulescent rosette in the vegetative state, and develop elongate stems bearing leaves, flowers and capsules in the reproductive state. The genus *Physaria* includes all except eight species previously recognized by various authors in *Lesquerella* S. Watson (e.g., Rollins and Shaw, 1973; Rollins, 1993, 1995; Rollins et al., 1996; Anderson et al., 1997; O'Kane, 1999). The species selected for this experiment included five wild species and five domesticated species, selected for high seed-yield (Table 1). Each group consists in a mixture of species with different life history: *Physaria mendocina* and *Physaria pinetorum*, are perennials;

Table 1

Wild and domesticated species of *Physaria* and *Oenothera* and their native area of distribution or selection.

Emergent group	Species and families	Native to (wild) or selected at (domesticated):
Wild	<i>Physaria gracilis</i> (Hooker) O'Kane & Al-Shehbaz (Brassicaceae)	Oklahoma and Texas, USA
	<i>Physaria pinetorum</i> (Wootton & Standley) O'Kane & Al-Shehbaz (Brassicaceae)	Arizona and New Mexico, USA
	<i>Physaria angustifolia</i> (Nuttall ex Torrey & A. Gray) O'Kane & Al-Shehbaz (Brassicaceae)	Oklahoma and Texas, USA
	<i>Oenothera mendocinensis</i> Gillies ex Hook. & Arn. (Onagraceae)	Central-West Argentina
	<i>Oenothera mendocinensis</i> x <i>O. odorata</i> (Onagraceae)	Central-West Argentina
Domesticated	<i>Physaria gracilis</i> (Brassicaceae)	Chubut River Valley, Argentina
	<i>Physaria pinetorum</i> (Brassicaceae)	Chubut River Valley, Argentina
	<i>Physaria angustifolia</i> (Brassicaceae)	Chubut River Valley, Argentina
	<i>Physaria mendocina</i> (Phil.) O'Kane & Al-Shehbaz (Brassicaceae)	Chubut River Valley, Argentina
	<i>Oenothera biennis</i> L. (Onagraceae)	India

Physaria angustifolia, and *Physaria gracilis* are annuals, *Oenothera mendocinensis* is annual or biennial and *Oenothera biennis* is biennial (Hoch, 1988). No description of the life history of *O. mendocinensis* × *O. odorata* is available. This is a natural occurring hybrid, which hereafter will be referred as “species” for the sake of simplicity. Despite these species had been described as annuals, biennial or perennials, some authors and our own field observations indicate that life history varies with resource availability and environmental conditions. For example, southern populations of *O. mendocinensis* produce seed during the first year, survive the winter and behave as iteroparous perennials, while northern populations behave as annuals (Vilela et al., 2008). Gimenez et al. (2013) reported that planting date, daylength extension and temperature affects reproductive behavior (annual or biennial) and the length of pre-flowering phase. Given the within-group variability, we used hierarchical clustering to divide objectively these species into two emergent groups (See details in Data Analysis and Supplementary Data). For further description of species see Boelcke and Romanczuk (1984), O’ Kane et al. (2004) and Rollins and Shaw (1973).

2.2. Study site and experimental conditions

A field experiment was performed in Gaiman, Chubut, Argentina (43° 21′ 31″ S; 65° 38′ 39″ W). This target area of cultivation is characterized by semi-desert Mediterranean conditions, with cold, wet winters and dry summers. Irrigation is possible from spring (September) to early fall (April). In this area the mean annual precipitation is 179 mm, mean low temperature of the coldest month (June and July) is 1 °C and absolute minimum air temperature is −10.8 °C. Seeds were sown mid-February in germination trays filled with soil, peat moss and sand in equal proportions and maintained in a greenhouse, where they received 80% of outside light levels and a temperature range of 25°/15 °C (average daytime/nighttime temperature). Seedlings were transplanted to the field 45 days after sowing (early April), in a completely randomized experiment with two factors: emergent group (domesticated and wild) and water availability (drought and non-limiting conditions). Experimental units consisted in plots (5 reps/emergent group/water availability). A plot included 20 plants/species, arranged in rows 0.30 cm apart and plants within a row were 0.15 cm apart. Density was low enough (15 pl m⁻²) to avoid detrimental effects of competition on final biomass, on the probability of flowering and on seed-yield (Brahim et al., 1998; Gambino and Vilela, 2011). Plants under non-limiting conditions were irrigated to field capacity every week. Plants under drought stress were irrigated when the rate of CO₂ assimilation was 50% lower than that of plants under non-limiting conditions (Vilela et al., 2003). The drought cycle length was around 25 days.

2.3. Traits measurements

Harvested plants were stored in plastic bags during transport to the lab. Total plant biomass was divided into roots, leaves and reproductive structures, dried a 70 °C for 48 h and weighed.

Reproductive biomass was calculated as the addition of seeds, fruits and reproductive support structures (Vilela et al., 2008) and reproductive effort (RE) as the ratio between reproductive and total biomass (Thompson and Stewart, 1981). RE is a measure of allocation to reproduction, similar to harvest index, widely used in agronomy. Root non-structural carbohydrate pool mass (TNC_{pool}) was calculated as root TNC concentration × root mass (Kobe et al., 2010) at the end of the growing season. TNC mass ratio (TNCMR) was calculated as TNC_{pool}/total biomass (g g⁻¹). Carbohydrates storage was measured in roots because this organ can store more

TNC reserves and it is a more sensitive measure of accumulated C reserves than the stems (Landhäuser et al., 2012; Vilela et al., 2012). TNC were determined by autoclaving (0.1 MPa, 15 min) 50 mg of biomass in 100 ml of distilled water. Polysaccharides (including starch) by this way are hydrolyzed into simple sugars. Dissolved sugars were determined by the anthrone method (Sadasivian and Manickam, 2010; Yemm and Willis, 1954).

Leaves mass ratio (LMR) and root mass ratio (RMR) were calculated as the proportion of total biomass allocated to leaves and roots, respectively. Once in the lab, leaves were placed in water for rehydration before specific leaf area (SLA) measurement (SLA > 10 m² kg⁻¹; Garnier et al., 2001). Leaf area was determined using Image Tool for Windows. After scanning, leaves were oven-dried until constant weight. SLA was calculated as the ratio between leaf area and leaf mass (Navas and Garnier, 2002).

2.4. Data analysis

A General Linear Models was specified for data analysis. In Table 2, we compared traits related to fitness (total biomass; reproductive biomass, reproductive effort and TNCMR) and traits related to plant adjustment to the environment (RMR; LMR and SLA) of wild and domesticated species grown under non-limiting and drought conditions. Data from all species within an emergent group (wild or domesticated) were combined to assess the effect of selection and water availability effect using a two-way ANOVA on the different variables measured. The interaction between selection and water was significant for all traits; therefore, the effect of selection was analyzed for each water treatment separately. In Table 2 a significant selection effect indicate differences between emergent groups for the same water treatment (non-limiting or drought). As wild and domesticated species differed in total biomass, we adopted a whole-plant perspective that incorporates effects of plant size (McConnaughay and Coleman, 1999; Weiner, 2004). Therefore, biomass was included in the model as a covariate to neutralize possible ontogenetic effects in the comparisons among emergent groups and treatments. A significant biomass effect indicates a size-dependent change. In Table 3, a significant water effect indicates differences in a trait due to water availability for each emergent group. The slopes of fitted curves (Fig. 1) were statistically compared between emergent groups using *F*-test.

In order to determine whether species within-groups reflected a natural correlation of biological attributes (i.e. emergent group; Lavorel et al., 1997), we conducted a PCA using the 10 taxa mentioned above and 6 traits: reproductive biomass, vegetative biomass, TNC_{pool}, RMR, TNCMR and RE. Only principal components (PCs) with eigenvalues higher than 1 were considered (Hautekete et al., 2009). PCA gave two PCs with eigenvalues higher than 1. The first component (PC1) was mainly structured by reproductive effort, RMR and TNCMR. PC1 was interpreted as an axis of resource allocation (i.e. trade-offs between reproduction and storage), accounting for 65% of total variance. At the lower end of this axis were species with high allocation to reproduction (domesticated species) and at the higher end were species with high allocation to storage and storage organs (wild species). PC2 accounted for 21% of total variance and was mainly structured by vegetative and reproductive biomass (Supplementary Table). We performed a hierarchical cluster analysis based on the eigenvectors calculated for PCA. Two groups of species were defined using Euclidean distance and Ward linkage (Supplementary Figure). We used InfoStat to perform cluster analysis.

In order to assess phenotypic plasticity, a relative distance plasticity index (RDPI) ranging from 0 (no plasticity) to 1 (maximal plasticity) was obtained for each trait, for selected and wild species. RDPI was calculated as $\sum [d_{ij} \rightarrow i'j' / (x_d + x_d)] / n$, where *n* is the

Table 2
General Linear Model (GLM) was applied for the effects of selection with total biomass (square root transformed) as a covariate. The effect of selection was evaluated for each water level because the interaction between selection and water was significant for all traits ($P < 0.05$; not shown). A significant selection effect indicates differences between wild and domesticated species for each water treatment. Interactions between selection and biomass were non-significant for every trait (not shown). GLM statistics are F-values. * = $p < 0.05$; *** = $p < 0.01$; ns = non-significant.

Traits	GLM for non-limiting conditions				GLM for drought			
	Wild	Domesticated	Selection effect	Biomass effect	Wild	Domesticated	Selection effect	Biomass effect
Total biomass (g plant ⁻¹)	9.51 ± 1.24	18.48 ± 1.54	17.36***	–	7.20 ± 0.75	9.23 ± 0.65	4.02*	–
Vegetative biomass (g plant ⁻¹)	1.64 ± 0.19	2.96 ± 0.20	14.65***	0.22 ^{ns}	2.79 ± 0.47	4.16 ± 0.33	9.94***	0.01 ^{ns}
Reproductive biomass (g plant ⁻¹)	3.46 ± 0.77	9.82 ± 1.00	10.07***	30.11***	2.37 ± 0.44	3.89 ± 0.47	8.51***	0.42 ^{ns}
TNC pool (g TNC _{root} plant ⁻¹)	0.09 ± 0.01	0.07 ± 0.02	1.88 ^{ns}	0.85 ^{ns}	0.08 ± 0.01	0.06 ± 0.01	3.77***	1.78 ^{ns}
Root mass ratio (RMR; g g ⁻¹)	0.07 ± 0.01	0.03 ± 0.01	18.00***	2.33 ^{ns}	0.09 ± 0.01	0.05 ± 0.01	21.04***	1.33 ^{ns}
Leaf mass ratio (LMR; g g ⁻¹)	0.14 ± 0.02	0.20 ± 0.01	7.64***	0.82 ^{ns}	0.21 ± 0.02	0.30 ± 0.01	15.52***	0.21 ^{ns}
Reproductive effort (RE; g g ⁻¹)	0.35 ± 0.05	0.51 ± 0.03	11.58***	1.37 ^{ns}	0.28 ± 0.03	0.40 ± 0.02	11.24***	0.27 ^{ns}
TNC % (% of root dry weight)	13.11 ± 1.10	13.71 ± 0.96	0.92 ^{ns}	6.44*	13.67 ± 0.94	12.53 ± 0.66	1.18 ^{ns}	0.20 ^{ns}
TNCMR (g g ⁻¹)	0.010 ± 0.002	0.004 ± 0.001	10.50***	1.28 ^{ns}	0.013 ± 0.001	0.007 ± 0.001	16.93***	4.83*
Specific leaf area (SLA; cm ² g ⁻¹)	108.62 ± 17.26	91.74 ± 9.69	0.02 ^{ns}	3.54 ^{ns}	85.54 ± 11.02	78.08 ± 5.01	0.04 ^{ns}	24.95***

Table 3
General linear model (GLM) for the effect of water availability on biomass accumulation and allocation traits of wild and domesticated, with total biomass (square root transformed) as a covariate. Mean trait values ± SE are included in Table 2. A significant water effect indicates a response of the trait to water availability and a significant biomass effect indicates size-dependent changes in the trait. Interactions between water and biomass were non-significant for every trait. GLM statistics are F-values. * = $P < 0.05$; *** = $P < 0.01$.

Traits	Wild		Domesticated	
	Water effect	Biomass effect	Water effect	Biomass effect
Total biomass	10.32***	–	43.71***	–
Vegetative biomass (g plant ⁻¹)	1.78 ^{ns}	0.05 ^{ns}	3.59*	0.19 ^{ns}
Reproductive biomass (g plant ⁻¹)	0.03 ^{ns}	105.28***	3.53 ^{ns}	241.21***
TNC _{pool} (g TNC plant ⁻¹)	0.23 ^{ns}	5.52*	0.11 ^{ns}	10.86***
Root mass ratio (RMR; g g ⁻¹)	0.004 ^{ns}	15.43***	1.92 ^{ns}	5.81*
Leaf mass ratio (LMR; g g ⁻¹)	5.12*	0.06 ^{ns}	24.27***	0.43 ^{ns}
Reproductive effort (RE; g g ⁻¹)	0.32 ^{ns}	4.44*	3.54*	0.83 ^{ns}
TNC % (% of root dry weight)	0.05 ^{ns}	0.001 ^{ns}	0.17 ^{ns}	3.89 ^{ns}
TNCMR (g g ⁻¹)	0.21 ^{ns}	6.35***	0.48 ^{ns}	1.09 ^{ns}
Specific leaf area (SLA; cm ² g ⁻¹)	0.37 ^{ns}	0.12 ^{ns}	15.54***	14.67***

total number of relative distances for a trait x . Each data was obtained by the absolute distance between two randomly replicates (j and j') of the same species and functional group growing under different water treatments (l and l'). Relative distances ($d_{ij} \rightarrow ij' / (xd + xd)$) were calculated for all possible pairs of replicates. This index gives an unbiased estimation of the levels of phenotypic variation and allows the exploration of plasticity with strong statistical power to test for differences in plasticity between genotypes and species (Valladares et al., 2006). One-way ANOVAs were performed to compare RDPI between functional group for each trait. Because RDPI ranges from 0 to 1, the index was arcsin-square root transformed prior to analysis.

3. Results

3.1. Resource-use strategy and association between traits

The comparison of biomass accumulation and allocation traits of wild and domesticated species indicated a shift in resource-use strategy, from conservative to acquisitive. Under non-limiting conditions (i.e. target cultivation environment), wild species were characterized by a suite of traits typical of species growing in

resource-poor habitats that favor conservation of resources, such as small plant size (low biomass) with high allocation to storage (TNCMR) and storage organs (RMR; Table 2). On the contrary, domesticated species showed a set of attributes typical of resource-acquisitive species: bigger plants with increased allocation to reproduction (reproductive biomass and RE) and leaves (LMR; Table 2). Specific leaf area (SLA), root TNC concentration and TNC_{pool} did not differ between groups.

Plant reproductive biomass was positively related to total biomass (Fig. 1A) and reproductive effort (Fig. 1B) for both wild and domesticated plants. The comparison of curves indicates that selection did not change the response slope ($F = 0.56$; $p = 0.85$ for Fig. 1A and $F = 2.37$; $p = 0.13$ for Fig. 1B); total plant biomass and RE at a given reproductive biomass was similar in both groups. Both groups showed trade-offs between the fitness proxy reproductive effort (RE) and the relative allocation to storage (TNCMR; Fig. 1C) and to storage organs (RMR; Fig. 1D). The response curve of domesticated plants did not differ of that of wild plants in neither relationship ($F = 0.56$; $p = 0.84$ and $F = 2.30$; $p = 0.12$, for Fig. 1C, D respectively).

3.2. Traits plasticity in response to water availability

Across environments, wild species showed higher homeostasis than domesticated species. Despite traits stability (non-significant water effect in most traits of Table 3), drought conditions provoked a 25% decrease of total biomass ($p < 0.01$). In turn, plant size affected reproduction, storage and storage organs (i.e. larger wild plants showed larger reproductive biomass, RE, TNC_{pool}, and lower RMR and TNCMR; biomass effect column in Table 3).

Domesticated species reduced their total biomass by 50% under drought conditions. The reduction in plant size also affected reproduction, storage and storage organs (Table 3; biomass effect) but unlikely wild plants, their RE were also affected by water availability (Table 3; water effect). Despite the lesser homeostasis across environments, domesticated species always showed within-environment bigger plants than wild species, with higher allocation to reproduction an lesser to storage and storage organs (Table 2; selection effects columns for non-limiting and drought conditions). Under drought conditions, the higher reduction of plant size and constancy in allocation to storage (TNCMR) resulted in domesticated plants with a pool of carbohydrate reserves (TNC_{pool}) significantly smaller than those of wild plants (Table 2). Selection did not affect SLA, although this trait showed size-dependent changes under drought conditions. Drought provoked an increased in LMR in both groups; this increment resulted from

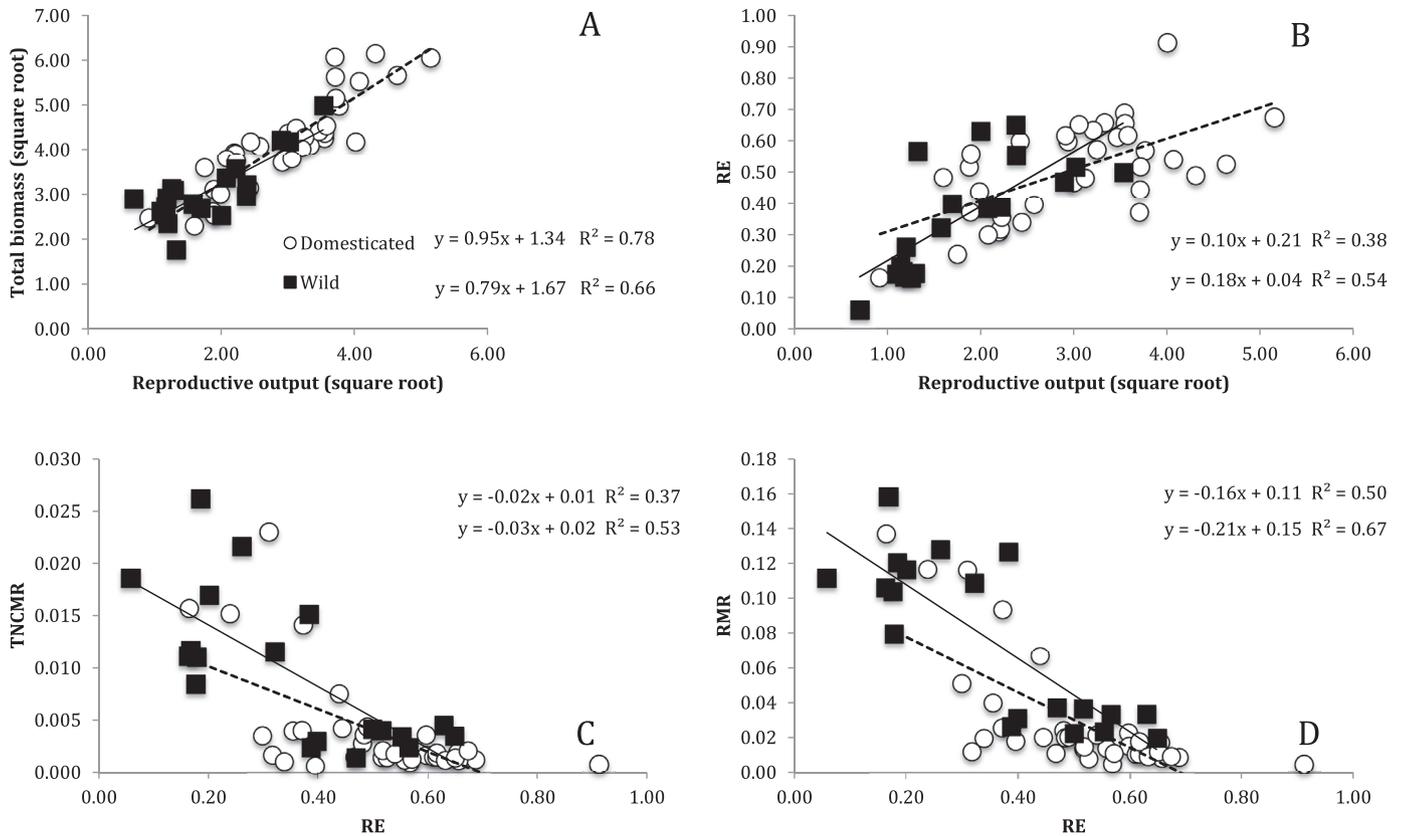


Fig. 1. Relationship between reproductive, growth and storage traits in wild (black square symbols) and domesticated (round open symbols) species. The upper R^2 values correspond to the regression line of domesticated species and the lower, to wild species.

a combined effect of increase in leaves biomass (g plant^{-1}) and decrease in RE.

The comparison of phenotypic plasticity of traits in response to water availability in wild and domesticated species indicated that selection significantly increased the plasticity of most traits (Table 4), except for those related to storage (TNC_{pool} and TNC%). The mean plasticity of wild plants traits was very low (<0.3) and significantly lower than that of domesticated plants ($P < 0.01$).

Table 4
Relative distance plasticity index (RDPI) for biomass accumulation and allocation traits estimated for wild and domesticated species and calculated across two treatments of water availability. The RDPI for traits followed by a different lower case letter are significantly different between plant groups ($P < 0.05$). Mean RDPI followed by different upper case letter are significantly different between plant groups. RMR = root mass ratio; LMR = leaf mass ratio; TNC pool = total pool of root non-structural carbohydrates (g); TNCMR = TNC mass ratio; RE = reproductive effort; SLA = specific leaf area.

Traits	Wild	Domesticated
Total biomass (g plant^{-1})	0.24 ^a	0.57 ^b
Vegetative biomass (g plant^{-1})	0.26 ^a	0.43 ^b
Reproductive biomass (g plant^{-1})	0.19 ^a	0.43 ^b
TNC pool ($\text{g TNC}_{\text{root}} \text{plant}^{-1}$)	0.37 ^a	0.39 ^a
Root mass ratio (RMR; g g^{-1})	0.13 ^a	0.23 ^b
Leaf mass ratio (LMR; g g^{-1})	0.21 ^a	0.47 ^b
Reproductive effort (RE; g g^{-1})	0.25 ^a	0.35 ^b
TNC% (% of root dry weight)	0.15 ^a	0.19 ^a
TNCMR (g g^{-1})	0.28 ^a	0.33 ^b
SLA	0.26 ^a	0.37 ^b
Mean	0.23^a	0.38^b

4. Discussion

4.1. Selection entailed a shift in resource-use strategy

We compared biomass accumulation and allocation patterns of wild and domesticated co-generic species, expecting groups to differ in their attributes and resource-use strategy because they were exposed to two different selection pressures. Predictably, wild species subjected to natural selection showed adaptations that allow a plant to survive through periods of environmental stress, such as freezing temperatures, constant low-humidity west winds and low mean annual rainfall (<200 mm) that characterized extra-Andean Patagonia. In this target cultivation environment, most rainfall events comprise less than 5 mm and the precipitation pattern results in a strong summer deficit (Paruelo et al., 1998). Irrigation usually compensates for fresh water scarcity, leading to unstable land uses and subsequent abandonment of large areas in a cycle of 50 years or less (Romo-Leon et al., 2014). In order to prevent these unsustainable management practices, the ability of a species to survive and produce seeds under harsh conditions should be considered as a criterion for selection of candidates to new crops domestication (Wassner et al., 2012). In our experiment, conservative wild species showed slow growth and preferential allocation of resources to storage and storage organs. Slow growth confers stress resistance by reducing carbon demands for growth, which thereby allows greater allocation to other process such as storage (Chapin et al., 1990; Wyka, 2000) that enhances survivorship under uncertain and fluctuating environments (Kobe et al., 2010) and endows frost tolerance (Kozłowski, 1992; Canham et al., 1999). On the contrary, domesticated species bred for high yield behaved as

acquisitive plants, investing resources preferentially to growth and reproduction.

The evolution of crops since their domestication has been driven by the selection of desired traits recognized at the phenotypic level (Cattivelli et al., 2008). Selection in cereals using yield as a selection criterion provided the desired result of increasing yield potential by way of a genetic shift towards greater harvest index (Blum, 2005). The positive relationship found between reproductive biomass and reproductive effort shows that this is also true for the species of our experiment: the use of high reproductive biomass as key selection criterion leads to increased reproductive effort.

On the other hand, selection for high yield generally does not increase total biomass but only the proportion between reproductive and vegetative structures (RE) within a given biomass (Blum, 2005; Vigouroux et al., 2011). Nonetheless, the small size of wild plants of *Physaria* and *Oenothera*, and the positive association between reproductive biomass and total biomass, might support the use of plant size as selection criterion for breeding programs in this experimental system, as it has been suggested for other *Oenothera* species (Vilela et al., 2008).

Associations of the target trait with other traits are likely to show up as correlated responses to selection (Scheiner, 2002; Brakefield, 2003). Fig. 1C, D shows trade-offs between allocation to reproduction and to storage (RE vs. RMR and TNCMR) in both groups of plants. The observed decrease of RMR and TNCMR in domesticated species is an indirect effect of selection, well matched with the breeders' goal of rising yield through increases in harvest index. These trade-offs arises when the production of reproductive structures is supported by translocation of carbohydrates from the vegetative part of the plant (Hirose et al., 2005) or when reproduction exhausts a particular nutrient or energy of the organism (Ehrlén and van Groenendael, 2001), thereby reducing its ability to accumulate stores (*sensu* Chapin et al., 1990).

LMR, on the other hand, was consistently lower in wild species. A reduced leaf area is associated with plant adaptability to drought-prone environments and lead to reduced yield potential (Fischer and Wood, 1979). This trait is one of the classical components of relative growth rate (RGR) because it greatly contributes to a larger carbon gain per unit plant weight (Lambers and Poorter, 2004; González-Paleo and Ravetta, 2011), increasing available resources for reproduction. The observed size-dependent increase of reproductive biomass (Table 2) can be explained because rosette plants increase their leaf area during reproduction and bigger plants are better able to continue growth during reproduction (Reekie, 1997). Despite SLA is generally a better predictor of RGR than LMR (Shipley, 2006) in our experimental system selection did not enlarge the former, but the latter.

4.2. Selection increased phenotypic plasticity: wild species showed higher homeostasis than their domesticated congeners

Plasticity of any given trait can evolve in response to selection (Via et al., 1995; Scheiner, 2002). Matesanz et al. (2010) advocated the use of artificial selection experiments to test the evolution of plasticity, because it is the best way to determine if and how fast a target trait will evolve under a given strength of selection. Our results indicated that domesticated species clearly outperformed their wild congeners in response to an increase in water supply, growing twice as fast and producing almost triple reproductive biomass. Besides these changes in traits mean values, a significant increase of plasticity in most traits was found. These results support the suggestion of Schlichting and Levin (1986) that the differentiation of plant taxa may involve changes in the plasticity of characters in addition to the commonly observed changes in character means.

Increased plasticity might be adaptive or injurious depending on whether changes are reversible or not over short time scales, which is the fitness proxy of the subject and environmental resource fluctuation (Martina and Von Ende, 2012). To be adaptive, plasticity should increase mean fitness across environments while it might be considered injurious if it leads to reverse changes under low-resource availability (Alpert and Simms, 2002). Our results indicate that across environments, domesticated species showed lesser homeostasis in allocation than their wild relatives but the reverse changes in biomass accumulation and reproductive effort were not complete. Despite overall changes in mean values, under drought conditions reproduction-related traits (reproductive biomass, total biomass and RE) remained higher and survival-related traits (TNCMR and RMR) lower in domesticated species than in their wild relatives. Considering that reproduction-related traits are used as fitness proxies for domesticated species, the increase in these traits plasticity might be adaptive for domesticated species. This is evidence that domesticated species conform to a "Master-of-some" strategy, in which the plasticity of morphological or physiological traits allows to take advantage of favorable environments. Contrariwise, wild species exhibited a Jack-of-all-trades strategy (i.e. better able to maintain fitness in a variety of environments; Richards et al., 2006), probably because the expenses incurred by maintaining the potential for being plastic (maintenance cost; DeWitt et al., 1998) in a homogeneous and predictable low-resource environment might constraint the evolution of phenotypic plasticity in wild species.

In summary, selection for high-yield shifted the resource-use strategy from conservative to acquisitive. The change in selection force from survival to reproduction provoked an increase in mean values of reproduction-related traits and a decrease in survival-related traits. This occurred concurrently with an increase in phenotypic plasticity of most traits and changes in the pattern of association between them. The improvement of reproductive traits was not completely reversible under low resource availability. The combination of higher values of advantageous traits and greater plasticity contributed to the success of domesticated species in plentiful environments.

Acknowledgements

This study was funded by Agencia Nacional de Promoción Científica y Tecnológica (PICT 2011 N°0598) and CONICET (PIP 112 20110100780).

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2014.09.005>.

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