

Phenological and morphological differentiation in annual *Chaetanthera moenchioides* (Asteraceae) over an aridity gradient

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Abstract Flowering-time, plant longevity and size of capitulum were studied in a common garden experiment on seven populations of annual *Chaetanthera moenchioides* derived from a strong latitudinal aridity gradient in the mediterranean climate area of Chile. Populations derived from the drier northern part of the latitudinal gradient showed significantly shorter flowering and fruiting phenology and smaller capitula under uniform growing conditions. Water stress experiments performed in the greenhouse induced further phenological hastening and a reduction in number of ray florets per capitulum. Population differentiation and the reaction norms in *C. moenchioides* agree with the predictions of genetic-assimilation given that the plastic response of the species under water stress mimics phenotypic differentiation that has evolved along the environmental gradient.

Keywords *Chaetanthera moenchioides* · Flowering time · Senescence · Aridity gradient · Water stress · Mediterranean climate · Genetic assimilation · Failure-time analysis

Introduction

Genetic assimilation is an evolutionary outcome by which part of a plastic response of a species becomes fixed in a population through time, resulting in the expression of that trait independently of the environmental cues that originally produced it (Pigliucci et al. 2006; Crispo 2007). Originally introduced by Waddington (1942), theoretical interest in genetic assimilation has been revived over the past years (Gerard et al. 1993; Behera 1994; Pal and Miklos 1999; Ancel 2000; Price et al. 2003; West-Eberhard 2003; Masel 2004; Badyaev 2005; Wiles et al. 2005; Lamm and Jablonka 2008), with emphasis on the circumstances and mechanisms under which an environmentally stimulated phenotype become a fixed response. The traditional explanation is that the selection of developmentally induced phenotypes eventually leads to the accumulation of alleles in a population that determine the propensity of an organism to produce that character. Organisms would then tend to concentrate more of these alleles over time until they finally would be able to trigger the character independent of the environmental cue (Waddington 1957; Braendl and Flatt 2006; Gómez-Mestre and Buchholz 2006). Other authors have focussed on the relevance of selective forces that act to avoid the costs related to the maintenance of developmental plasticity mechanisms, favouring the persistence of genes that mimic ‘the adequate plastic response’ under a given environment (Simpson 1953; Behera 1994; Mayley 1996; de Witt et al. 1998; Dorn et al. 2000; van Buskirk 2000; Van Kleunen et al. 2001; Relyea 2002; Van Kleunen and Fischer 2005). Nonselective mechanisms underlying fixation of environmental-induced characters comprise epigenetic inheritance systems (Jablonka and Lamb 1995; Pal and Miklos 1999; Jablonka 2007; Badyaev and Oh 2008), which are also

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known as ‘transgenerational plasticity’ (Lamm and Jablonka 2008). Furthermore, Masel (2004) recently proposed that plastic characters could become fixed in a population by chance assuming the Waddingtonian “canalization heuristic”.

Although much empirical evidence is consistent with the genetic assimilation framework (Pigliucci and Murren 2003; West-Eberhard 2003; Adams and Huntingford 2004; Heil et al. 2004; Braendl and Flatt 2006; Gómez-Mestre and Buchholz 2006; Pigliucci et al. 2006; Badyaev 2007), critical research on genetic assimilation in natural populations is scarce (Pigliucci and Murren 2003; Lamm and Jablonka 2008). Our understanding of the actual occurrence of genetic assimilation in nature, the environmental circumstances, time lapses involved, and organisms and attributes affected, is poor.

Because genetic assimilation supposes a shift in the reaction norm of populations through time (Pigliucci and Murren 2003), studies are badly needed on natural variability among populations of the same species growing under differing environmental conditions. In this respect, the phenology of plants in relation to water availability provides an attractive case. Populations of a species are known to flower earlier under higher water stress (Fox 1990a; Bennington and McGraw 1995; Petit and Thomson 1998; Heschel and Riginos 2005; Franke et al. 2006), there being notable cases described for serpentine soil-related environments (Schmitt 1983; Brady et al. 2005), mining areas (Jowett 1964; McNeilly and Antonovics 1968), and along extensive latitudinal gradients (Del Pozo et al. 2002). Different amounts of precipitation received in different parts of a geographical region leads to similar consequences among populations (Shinoda et al. 2007; Palta et al. 2007). However, several case studies have shown that such phenological differentiation cannot be solely explained as a plastic response, as differences in the ecotypes are maintained under transplant or common garden experiments (McNeilly and Antonovics 1968; Linhart 1973; Fox 1990a; Rice and Mack 1991a, b; Aronson et al. 1992; Bennington and McGraw 1995; Del Pozo et al. 2000; Heschel and Riginos 2005; Franke et al. 2006; Sambatti and Rice 2006; Ofir and Kigel 2006; Franks et al. 2007; Sambatti and Rice 2007). Genetic assimilation for advance of flowering time in populations colonizing drier environments (or its delay in population colonizing wetter conditions) could occur if environmentally mediated (plastic) advance or retardation in flowering time, respectively, occurs in some part of the species range from whence the water-stressed (or water-saturated) populations evolved. Indirect evidence for this hypothesis would consist of showing that the reaction norm of the derived (actual) populations parallels the evolved scenario

(Pigliucci and Murren 2003; Aubret et al. 2007). That is, if water stress (or excess water) is capable of plastically hastening (or retarding) flowering time in present-day populations, it is plausible that it had also done so in the past. Presently there is no consensus about the relation of flowering time and water stress. It has been empirically shown that water stress can hasten (Rice and Mack 1991b; Aronson et al. 1992; Bennington and McGraw 1995; Rajakaruna et al. 2003; Sherrard and Maherali 2006) or retard flowering time (Fox 1990b; Steyn et al. 1996; Berg et al. 2005; Caruso 2006), or even have neutral or contradictory effects (Steyn et al. 1996; Heschel and Riginos 2005; Van Kleunen 2007). Some of the ambiguity in this area may relate to the difficulty of standardizing water-stress methodologies, i.e. timing, kind and intensity of the stimulus to be applied.

In the mediterranean-type climate of central Chile, a rich and diverse native annual flora occurs over a severe aridity gradient (Arroyo et al. 1995). Soils in central Chile reach field capacity during the winter rains and begin to dry in late Winter (August) in the North and in late Spring in the South (December). *Chaetanthera moenchioides* Less. (Asteraceae), an endemic annual distributed over this climatic gradient, presents a shifting in its phenology in relation to this moisture variation. Casual observations made in the Spring of 2002 revealed that *C. moenchioides* flowers in late September at around 30°S in the northern extreme of its range, whereas at the southern boundary of its distribution, some 1,100 km to the South, flowering commences in the second half of November, the size of the southern plants also larger.

To investigate whether variation in the phenology of *C. moenchioides* could correspond to a case of evolution mediated by genetic assimilation, we performed a common garden experiment in which plants of the species drawn from over 600 km of its geographical range were submitted to different moisture conditions, applying a humid regime and desiccating stimuli at different times in the plant’s ontogeny. If flowering time in *C. moenchioides* had evolved through genetic assimilation in response to moisture conditions, we would expect that; (1) existing differences in flowering time among populations remain, at least in part, under homogenous growing conditions, and (2) applied water stress produces further hastening in flowering time. Since a shift in flowering time supposes a modification in developmental-timing, the morphology and longevity of the plant are expected to shift in concert with flowering time (Noodén 1980; Battjes and Bachmann 1994; Zopfi 1995; Li and Johnston 2000; Barth et al. 2006). To test this last prediction, we monitored the time of senescence and capitulum size in *C. moenchioides* under the experimental treatments.

Materials and methods

Focal species and study sites

Chaetanthera moenchioides is an endemic annual (ca. 5–20 cm tall) with small yellow capitula, showing high levels of spontaneous selfing (Arroyo and Uslar 1993; Fig. 2). It is distributed throughout central Chile (30°–39°S), commonly in the 600–1,000 m.a.s.l. elevation range, where it forms large and continuous populations in the open spaces between trees and shrubs of typical sclerophyllous (matorral) vegetation.

Seven matorral populations of *C. moenchioides* were selected between latitudes 30 and 36°S (Table 1). Populations were evenly distributed along the gradient and were chosen so as to limit altitude and habitat variation. Bulk seed collections were made in each population in the austral spring of 2002 and stored in paper bags in the laboratory. Precipitation and evapotranspiration data for weather stations nearest to the studied populations are given in Fig. 1.

Experimental procedure

To ensure complete after-ripening, seeds were placed in an incubator for 2 weeks at 40°C. Seeds were germinated on wet paper in Petri dishes under light in a laboratory refrigerator. Seedlings were transplanted from the pool of germinating seeds into trays in a greenhouse located in Santiago, 33°S. A 1:1 mix of fine sand with sterilized and sieved native soil was used as a growth substrate. At the beginning of July (austral winter), 919 individuals were successfully transplanted (Table 1). Each tray contained a random selection of individuals from each of the seven populations and was assigned to one of the four watering treatments (see below). This resulted in a factorial experimental design of 28 treatments with an average initial sample size per treatment per population of 33 plants.

Table 1 Location data, altitude and acronyms for populations of *C. moenchioides*

Population	Acronym	Altitude (m.a.s.l.)	Latitude S (°)	Long W (°)
Vicuña	VIC	1,050	30°06'	70°42'
Combarbalá	COM	960	31°08'	71°05'
Cuncumén	CUN	1,092	31°56'	70°36'
Colina	COL	1,075	33°11'	70°35'
Cauquenes	CAU	1,000	34°15'	70°32'
Curicó	CUR	600	34°58'	70°58'
Talca	TAL	990	35°48'	70°56'

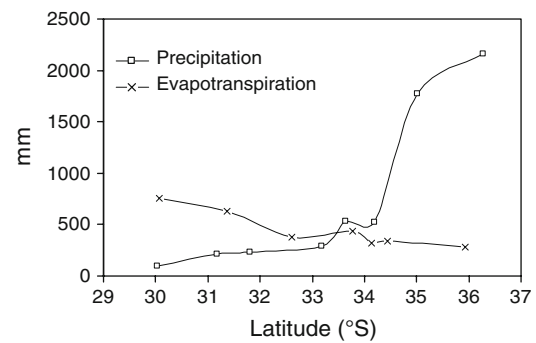


Fig. 1 Annual precipitation (boxes) and evapotranspiration (crosses) between May and October (austral winter-spring) in the mediterranean-type climate of central Chile. Stations are those closest available to the populations of *C. moenchioides* studied. Precipitation data taken from Ramírez and Lucabeche (2001). Evapotranspiration data taken from Dirección Meteorológica de Chile (1988–2001)

For the first eight weeks of the experiment, all plants received abundant water through periodic flotation of the trays over water, so as to ensure that the substrate remained permanently at field capacity: above -15 cbar of soil humidity tension (Larcher 1995). Watering to field capacity ceased in the trays assigned to the treatments Dry 1, Dry 2 and Dry 3 after 8, 12 and 16 weeks, respectively, so as to produce a water stress effect at three different points in plant development. Plants in the last three treatments from then on were watered by flotation for periods of three minutes. The remaining trays, comprising the humid treatment, were maintained at field capacity for the whole experiment and thus were never desiccated. Soil humidity was regularly evaluated with a mechanical IRROMETER tensiometer model ISR-600 (IROMETER Co., Riverside, California) in order to gauge the frequency of watering. Mean soil humidity of the plants under field capacity averaged a tension of -11.9 cbar (SE = 0.49; $n = 379$). Mean soil water tension of the substrates after dissection was -35.3 cbar (SE = 1.10; $n = 339$). The average soil tension values of the Dry 1, Dry 2 and Dry 3 treatments did not differ (ANOVA $F_{2, 335} = 1.93$, $P = 0.15$), the time of the dissection being the sole difference between them (Fig. 3).

Plant characteristics measured

We regularly monitored the experimental plants for opening of the capitulum and infrutescence and the number of ligules per capitulum and summarized the data at weekly intervals. Accordingly, the date of first flowering was defined as the number of weeks after transplantation to the time of opening of a plant's first capitulum, and the date of senescence as the number of weeks to appearance of the last infrutescence. We chose the particular manifestation of plant senescence because the plants were evidently

withering at this point (c.f. Noodén et al. 2004). Of the initial 919 plants, 393 produced flowers and were included in the time to flowering analysis. For 61 of these plants, we were unable to estimate senescence time as the capitulum did not produce seeds. The ray florets present in the first mature capitulum was also assessed; however, data could not be obtained for 38 individuals, because on such plants the first flowering capitulum was already well closed on the observation day.

Data analysis

The time to first flowering and time to senescence were analysed with an accelerated failure time analysis with the LIFEREG procedure in SAS (version 9.1; SAS Institute, Cary, NC, USA). This analysis evaluates both the phenological time function and if a survival function fitted to the data is shifted to the left or to the right by covariates. We used population and watering treatment as covariates in the model and specified a gamma distribution (Fox 1990a). As the time to senescence is correlated with time to flowering, we used the latter as a covariate in the analysis of time to senescence. For further comparisons among the levels of each factor ($P < 0.05$) we performed pairwise comparisons as per Fox (2001).

Observations could not be carried out during the last day of weeks 13 and 16, so the information concerning the respective next measuring day was handled as interval censored data.

After a square-root transformation, the number of ray floret was analyzed with a factorial ANOVA (7 populations \times 4 treatments) using watering treatment and population origin as fixed factors. Differences between levels of the factors were detected with Tukey a posteriori tests.

Results

Failure time analysis showed that the population origin and watering treatment had significant effects both on the time of first flowering and longevity of *C. moenchioides* (Table 2). Northern populations from the drier end of the gradient tended to open their first capitula earlier than the southern populations from the wetter end of the gradient, with a 4-week difference between the median values for the latitudinally extreme populations (Fig. 2). The a posteriori analysis showed that the significant effect of the watering factor was explained solely by the humid treatment, which slowed anthesis of the plants by 1 week, in comparison to the other dry treatments (Fig. 2b). This behaviour was general in the populations, as the interaction factor was not significant in the analysis (Table 2, Fig. 2a). The influence of watering treatment on the time of senescence was more

Table 2 Accelerated failure time analysis for time to flowering and senescence

Parameter	DF	β	SE	χ^2	P
Time to flower					
Intercept	1	29.18	0.015	45408.70	<0.001
Population	6			6914.15	<0.001
Watering	3			127.03	0.005
Population \times watering	18			199.32	0.337
Scale	1	0.06	0.002		
Shape	1	-0.05	0.083		
Time to senescence					
Intercept	1	29.45	0.054	3034.52	<0.001
Population	6			269.94	<0.001
Watering	3			5495.07	<0.001
Flowering time	1			176.43	<0.001
Population \times watering	18			467.48	<0.001
Scale	1	0.05	0.002		
Shape	1	0.37	0.129		

The bold entries are the P values that grant significance to the respective factors at the 0.05 level

intense (Fig. 3). While the differences in longevity among populations diminished, the plants growing under continuous soil humidity saturation experienced 3–4 weeks longer life-spans than the plants subjected to water stress. The response of the populations, although uniform in direction, was not uniform in intensity (Fig. 3), producing a significant interaction factor in the analysis (Table 2).

The ANOVA on ray floret number showed similar results as the phenology analysis, with both latitude and watering treatment affecting these variables (Table 3). Under the Dry 1 treatment, the first capitulum contained an average of 2.1 ligules, while under the rest of the treatments (no significant differences among them), the average number was 2.9. A progressive increase in ligule number toward the south of the gradient was observed (Fig. 4), together with increasing sensibility of the plants to water stress.

Discussion

We found evidence that the phenology and capitulum size of *C. moenchioides* has evolved along the geographical gradient of central Chile matching the prediction of a genetic assimilation outcome. Since we observed overall phenological shortening and reduction in capitulum size in *C. moenchioides* under water stress, it is plausible that putative ancestral populations of the species that colonized the more arid zones of central Chile previously experienced plastic variation in these traits before they became fixed. Reduction in life span seems to have occurred frequently in the evolution of desert annuals (Kannenberg and Allard

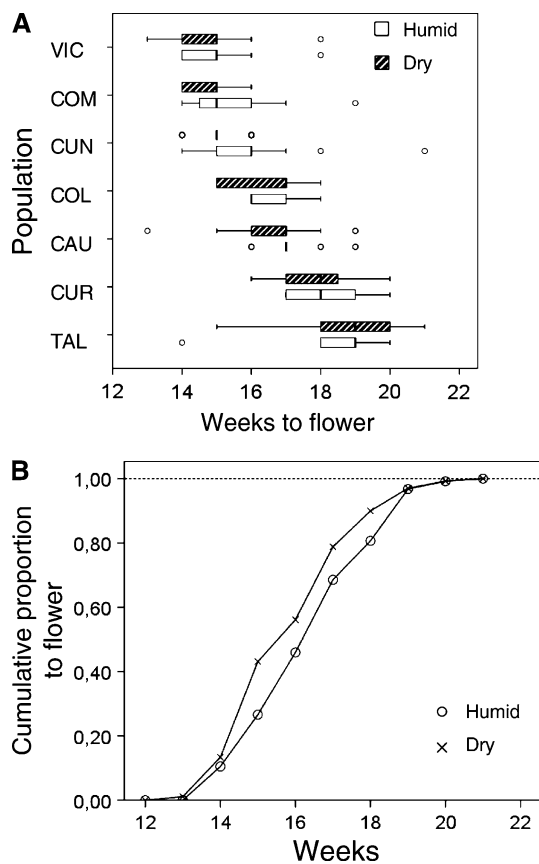


Fig. 2 Time to first flowering in *C. moenchioides*. **a** Boxplot of the time to first flowering per watering and population. The *thick bar* represents the median, the *box* indicates the 25–75th percentiles, whiskers are the lower and upper outlier border and the *circles* denote extreme values. Populations are arranged from the northernmost (up, driest natural conditions) to the southernmost (down, wettest natural conditions). For each population are two *bars* showed: the uppermost represents the Dry treatments pulled together (a posteriori tests reported no significant differences among them, see text) and the inferior the humid treatment. **b** Accumulated proportion of plants opening the first capitulum through the experiment. *Crosses* represent the three Dry time treatments and *circles* the humid treatment. Failure time analysis showed a significant retardation of the flowering time (see text)

1965; Rathcke and Lacey 1985; Fox 1990a), leading to the formation of races or sister species (Monson and Szareck 1981; Rajakaruna and Bohm 1999; Gardner and Macnair 2000; Brady et al. 2005). Alternatively, the southern populations of *C. moenchioides* could be considered as derived, in which case the original phenology of northern populations would have become more extended over time. An analogous case has been described for the annual *Abronia angustifolia*, where perennial variants have evolved under higher natural water supplies (Royce and Cunningham 1982).

The differences in flowering time observed in the greenhouse in *C. moenchioides* are less pronounced than in the field, suggesting that natural phenological differentiation of *C. moenchioides* along the latitudinal aridity

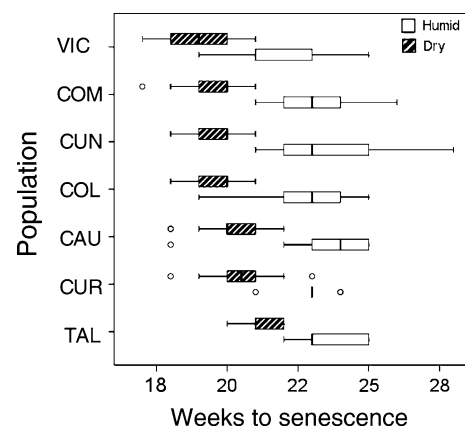


Fig. 3 Boxplot of the time to senescence in *C. moenchioides*. Sequence of boxplots and signatures as in Fig. 2

Table 3 Factorial two-Way ANOVAs for number of ray florets in *C. moenchioides*

Parameter	SS	DF	SM	F	P
Population	2.413	3	0.804	6.381	<0.001
Watering	31.175	6	5.196	41.218	<0.001
Population × watering	2.161	18	0.120	0.952	0.515
Error	41.221	327	0.126		

The bold entries are the *P* values that grant significance to the respective factors at the 0.05 level

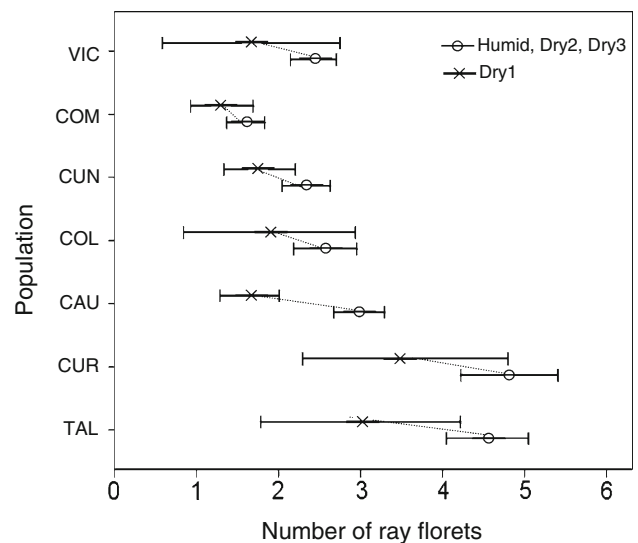


Fig. 4 Mean number of ray florets in first capitulum of *C. moenchioides*. *Bars* represent 95% confidence intervals. Populations are arranged from north to south showing both Dry 1 (uppermost) and the resting watering treatments pooled together (Tukey a posteriori test did not show significant differences among them)

gradient might also be influenced by other environmental factors such as temperature and photoperiod affecting growth and the time of seed germination. In this regard, the longer photoperiods and the higher temperatures occurring

in more equatorial areas in the spring could act as environmental cues that trigger earlier flowering (Tan and Swain 2006). Under cooler temperatures at the southern extreme of its distribution, germination is likely to occur at a later date than in the more northerly populations. Thus the phenological differentiation in flowering seen in the field has two components—an evolved response, in turn, overlain by an environmental response. Reciprocal transplant experiments are needed for precise determination of the contributions of these two components.

The production of more ray flowers per capitulum in the southern populations under uniform growing conditions was correlated with later flowering time. Battjes and Bachmann (1994) found that individuals of the *Microseris* (Asteraceae) produced larger floral parts as a consequence of the thicker meristem that they acquired when growing at a slower rate. Hence, large organ size together with a delay in the phenology, as seen in the more southerly populations of *C. moenchioides* in the common garden experiment could be explained by slower developmental rates during ontogeny. Such ‘big late-maturing plants’ have been documented in other studies (Barrett and Wilson 1980; Monson and Szareck 1981; Aronson et al. 1992; Winn and Gross 1993; Olsson and Agren 2002; Rajakaruna et al. 2003).

Overall we found reduced longevity on earlier flowering plants which corroborates the relation proposed between time to flowering and plant senescence (Noodén et al. 2004; Barth et al. 2006). Nevertheless, the fact that the time to senescence was also significantly affected by both watering and population treatment shows that longevity in *C. moenchioides* can not be solely explained by modification of the time of inception of flowering. Moreover, the intensity with which the longevity of *C. moenchioides* was reduced under water stress also varied among populations, as the interaction term in the analysis of time to senescence was significant. This indicates that environmental cues acting after flowering are also important in determining the time of senescence in *C. moenchioides*.

Our results show that the water stress affected the time to senescence more acutely than the time to flowering (Figs. 2, 3). This is concordant with Zhang and Lechowicz (1994), who showed that degree of plasticity in post floral traits is higher than in pre-floral traits in *Arabidopsis thaliana* (Brassicaceae). Analogous observations have been made by other authors (Reader 1982; Aronson et al. 1992; Winn and Gross 1993). Phenology differed between the humid versus and the rest of the Dry treatments, to the extent that the time of desiccation was irrelevant for flowering or senescence time. This suggests that dissection per se, rather than its duration, is responsible for hastening flowering time. A ‘cumulative effect’ of water stress could nevertheless be responsible for the higher

plastic response in time to senescence, as after flowering, the plants under the three dry treatments continued experiencing water shrinkage until they died. A cumulative effect of water stress on capitulum morphology is also apparent, since the number of ligules was modified solely under the Dry 1 treatment.

A critical question in the case of *C. moenchioides* concerns whether the life cycle has been shortened at the northern end of its distribution, or lengthened at its southern extreme. An answer to this question requires access to phylogenetic and phylogeographic information. Recent molecular phylogenetic construction of the genus *Chaetanthera* (Hershkovitz et al. 2006) forthcoming after completion of the experiment work shows that the sister group of the clade containing *C. moenchioides* comprises two mid-high elevation annuals from arid habitats in Peru, both with short life-cycles. The latter would suggest a lengthening of the life-cycle in the southernmost populations of *C. moenchioides* in relation to the northernmost populations, although until a comparative study of the sister group species and the northern populations of *C. moenchioides* has been undertaken, it cannot be fully ascertained that some shortening of the life-cycle in the northern populations has not also taken place. On the other hand, the clade containing *C. moenchioides* contains several long-lived perennial species, such that the annual habit in *C. moenchioides* could have been derived proximally from an intermediate perennial ancestor within that clade, with subsequent shortening of the life-cycle in the northern part of the species distribution. Until the clade containing *C. moenchioides* can be better resolved, the answer to this critical question remains equivocal.

Pigliucci and Murren (2003) cite several studies for plants that agree with our data and also suggest fixation of plastic ecological modification, such as plant growth-form and habit (van Tienderen 1990) and foliar morphology and plant size (Gurevitch 1988; Gurevitch 1992). At the same time, evidence has been found in plants for intergenerational maintenance of environmental modification through epigenetic inheritance systems known as environmentally induced ‘maternal effects’ (Mousseau and Fox 1998; Bernardo and Agosta 2005; Durrant 1958; Schweitzer and Ries 1969; Potvin and Charest 1991; Rossiter 1996; Seligmann 1997; Van-Zandt and Mopper 2004; Agrawal 2001). The latter offers a possible mechanistic explanation for the maintenance of environmental modification in the phenology in *Chaetanthera*.

Although the mechanisms behind genetic assimilation are clearly complex, the study of its possible occurrence and frequency in nature can provide understanding of evolutionary patterns along environmental gradients. When maternal effects are involved, rapid evolutionary responses can be expected. Better understanding of genetic

assimilation and underlying mechanisms is highly relevant to predictions of plant responses under climate change, especially in short-lived species.

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