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Leaf morphological responses to variation in water availability for plants in the *Piriqueta caroliniana* complex

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Abstract Distribution of plants and the expression of traits associated with environmental variation can be affected by both average conditions and the variance in conditions including extreme climatic events. We expect that these same factors should affect the distribution of plants in hybrid zones between ecologically distinct species where the hybrids should occupy ecotones or intermediate habitats. We evaluated water availability and leaf morphological differences among parental and hybrid populations of herbaceous perennial plants in the *Piriqueta caroliniana* complex along environmental gradients in Southeastern North America. We focus on two taxa in this group; the *viridis* morphotype, which occurs in southern Florida, and the *caroliniana* morphotype, which is distributed from northern Florida to southern Georgia. Advanced-generation hybrid derivatives of these morphotypes occupy a broad geographic region that extends across much of central Florida. Overall, we found that hybrid populations occurred in significantly drier locations, indicating that their habitat requirements are transgressive (i.e., exceeding parental values) rather than intermediate to the parental morphotypes. Water availability differed between the two sampling years, and plants displayed morphological changes in response to these changes in moisture. During the drier year, leaves were narrower and more hirsute, corroborating experimental results that these leaf traits are plastic, and confirming that plasticity occurs in natural habitats. Hybrids exhibited intermediate leaf traits (shape and size) across both years, and displayed transgressive (hair density) leaf traits during the drier year. The apparent canalization of the hybrids' leaf morphological traits may contribute to their tolerance of variable environmental conditions and may partially explain why they have displaced the *caroliniana* morphotype in central Florida.

Keywords Hybrid · Plasticity · Leaf trichomes · Leaf shape · Natural populations · Transgressive traits

Introduction

Species' distributions are influenced by their tolerance of local ecological conditions (Clausen et al. 1941; Levin and Schmidt 1985; Meekins and McCarthy 2000). Morphological and physiological traits that have evolved in response to specific environmental

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conditions may be responsible for the ability of plants to survive and reproduce in different habitats (reviewed in Bazzaz 1991). Temporal variation in ecological conditions may also influence plant distributions if environmental fluctuations result in conditions exceeding the species' tolerance limits (Bazzaz 1991). A large number of studies have documented the ability of plants to exhibit phenotypic plasticity (i.e., changes in traits in response to the environment) in controlled experiments (reviewed in Pigliucci 2001) or reciprocal transplant studies (Clausen et al. 1941; Dudley and Schmitt 1996; Maron et al. 2007; Warren et al. 2006; Williams et al. 1995), but examples of plastic responses of natural populations to environmental variation in native habitats are rare (see Callahan and Pigliucci 2002; Galen and Stanton 1995 for notable exceptions). Examining environmental variation and phenotypic responses of plants in the field is important to document plastic responses under natural conditions and to assess the adaptive value of plasticity to changes in environmental conditions.

Plant success in a given environment is often dependent on water availability (Galmes et al. 2004; Volaire et al. 1998). If plants do not have adequate access to water, then rates of photosynthesis are reduced, and persistent drought can prove fatal (reviewed in Boyer 1976). The amount of heat, plants are subjected to can affect their rate of evapotranspiration (Givnish and Vermeij 1976), and higher temperatures result in increased rates of water loss, thereby effectively altering plants' water use efficiency (Parkhurst and Loucks 1972).

Many plants have characteristics enabling them to tolerate drought (Schmidt and Levin 1985). Plants often have physiological or morphological traits (e.g., smaller leaf size and increased trichome density) that prevent excessive water loss and allow them to survive in arid environments (reviewed in Nobel 1999). Plants may also be able to alter characteristics of above-ground (shoots and leaves) and/or below-ground (roots) organs throughout the growing season (plasticity) as a stress response to water availability (Chidumayo 2006; Koike et al. 2003). Although plastic responses of phenotypic traits may increase plants' ability to survive water stress, there may also be a fitness cost. Since morphological modifications incur the use of both resources (nitrogen, phosphorous, etc.) and energy (carbohydrates; reviewed in van Kleunen and Fischer 2005), it is important to understand the adaptive value of such trait changes in response to variable water availability.

Hybrid offspring of species associated with different habitats may be able to tolerate intermediate environmental conditions that are unfavorable to both parental genotypes (Anderson 1949). Several studies have found that hybrids are located within or perform better in intermediate habitats (dePamphilis and Wyatt 1989; Freeman et al. 1991; Heywood 1986; Kentner and Mesler 2000; Rolan-Alvarez et al. 1997); however, hybrids may also occur in the same habitat with the parental species (Burgess and Husband 2006), or occupy habitats that are dissimilar to those of the parental genotypes (Arnold 1993; Cruzan and Arnold 1993; Neuffer et al. 1999; Rieseberg et al. 1990). These different scenarios will contribute to the survival and evolution of the hybrid trait expression (see Rieseberg and Carney 1998 for a review of hybridization). Hybrids may exhibit intermediate, new, or transgressive (i.e., exceeding the range of trait expression found in parental genotypes) traits that may allow them to tolerate environmental stressors thereby resulting in the expansion of hybrids into new habitats (reviewed in Rieseberg et al. 2007). In this study we will focus on the ways in which members of an herbaceous hybridizing plant species complex (*Piriqueta caroliniana*) undergo alterations in leaf morphology in response to fluctuating water availability, and the possible implications of how these morphological differences may have affected the current distribution of the parental taxa and hybrids.

Previous common garden and greenhouse experiments have documented that the two morphotypes (defined here as morphologically and ecologically distinct taxa; Martin and Cruzan 1999) and their hybrid derivatives exhibit plastic leaf traits (size, shape, and trichome density), with leaves becoming narrower and hairier in response to decreasing moisture availability (Picotte et al. 2007; A. Henderson and M. B. Cruzan, unpublished data). However, the degree of variation and plasticities of these leaf traits for plants in natural populations have not been documented. In this study we examine differences in water availability and the response of morphological trait expression for plants in natural populations of morphotypes within the *Piriqueta caroliniana* complex, including *caroliniana* (C), *viridis* (V), and advanced-generation recombinant hybrids (H). Specifically we address the following questions: (1) Does water availability differ among *viridis*, *caroliniana*, and hybrid habitats? (2) Are environmental conditions of hybrids intermediate or transgressive relative to parental habitats? (3) Do leaf traits that are associated with drought tolerance (leaf area, width/length ratio, and trichome density) differ between years? and (4) Do changes in leaf traits (plasticity) correlate with water availability?

Materials and methods

Study system

Plants in the *Piriqueta caroliniana* Urban (Turneraceae) complex (*P. cistoides* ssp. *caroliniana*; Arbo 1995) are herbaceous, perennial flowering plants that occur in tropical and sub-tropical regions of the New World. Plants in this complex are represented by several morphotypes and hybrid zones occurring within South and Central Florida (Maskas and Cruzan 2000). Populations sampled for this study include the *viridis* (V) morphotype, which occurs in the poorly drained, periodically flooded, calcium sands of South Florida, and the *caroliniana* morphotype (C), which grows in the well-drained quartz sand soils of North Florida and South Georgia (Maskas and Cruzan 2000). A broad hybrid zone extends across Central Florida, where habitats range from the xeric sandhills of the Lake Wales Ridge to the more mesic palmetto flatwoods (Fig. 1; see Abrahamson and Hartnett 1990; Myers 1990 for habitat descriptions). These hybrid populations (H) were derived from natural hybridization between the C and V morphotypes (Martin and Cruzan 1999), and populations across the hybrid zone differ with respect to both, time since initial hybridization and degree of isolation from allopatric populations (Cruzan 2005).

The ecological differences across *Piriqueta* habitats may have selected for variations in leaf morphologies observed among C, V, and H populations in Florida and South Georgia. Leaves of the C morphotype are relatively short (mean = 3.15 cm), wide (mean = 1.02 cm), and are densely covered with hirsute and stellate pubescence. The V morphotype, on the other hand, bears leaves that are relatively long (average = 3.72 cm), narrow (average = 0.15 cm), and completely hairless. Advanced-generation hybrids from Central Florida populations possess leaves exhibiting transgressive or intermediate morphologies relative to typical *viridis* and *caroliniana* leaves (Martin and Cruzan 1999; Picotte et al. 2007).

Fig. 1 Map of distribution of weather stations and *caroliniana* (C), *viridis* (V), and advanced generation hybrid (H) populations within the *Piriqueta caroliniana* complex in Florida and southern Georgia

Climatic differences among sites

We obtained interpolated climate data (including 30-year averages, monthly temperature averages, and total monthly precipitation during 2004 and 2005) from the Prism Group, Oregon State University (http://www.prismclimate.org, created 10/22/2007) for populations of the *Piriqueta caroliniana* complex (Fig. 1). Average temperature and precipitation over a 30-year period, and in 2004 and 2005, were also used to calculate the potential evapotranspiration (PET) for each site using Malmstrom's (1969) method. PET estimates the maximum amount of evapotranspiration of a given area under ideal conditions (including unlimited plant access to soil water, a surrounding area that is completely vegetated, and no air heat advection effects) using the formula:

$$\mathrm{PET} = 40.9 \times e_s(T_a)$$

where $e_s(T_a)$ is the saturation vapor pressure at the mean daily temperature at each site (Malmstrom 1969). The aridity (A) of each site was calculated with the formula:

$$A = P/\mathrm{PET}$$

where P was the precipitation and PET was the monthly potential evapotranspiration at each site (Budyko 1974; Thornthwaite 1948).

Phenotypic plasticity in natural populations

To determine each population's leaf morphological characters, a fully-expanded leaf was taken from the previous month's growth. Earlier greenhouse experiments have determined that C, V, and H plants generally add one node of growth per week (unpublished data). Taking the leaf from the fifth node counting down from the flower allowed the systematic collection of a leaf from the previous month's growth. Leaf samples were obtained from a maximum of 40 plants at each of the 19 populations (7 C, 2 V, and 10 H sites with at least 10 plants present) sampled in July 2004 and 2005. The discrepancy in the number of H and C versus V populations is the result of the extirpation (often due to land development) of V populations between 2004 and 2005. Leaf specimens from both years were then pressed in coin envelopes and allowed to dry. Leaves from each respective season were photographed at Portland State University with a Panasonic GCD® digital camera for leaf length, width and area; leaves were photographed with a Leica® MZ16 dissecting microscope and Q-Imaging® Retisa 1300 digital camera at 40X magnification to obtain images for the estimation of trichome density. All images were analyzed using Image-Pro Plus® v5.1. We estimated trichome density of the underside of each leaf by counting the total number of hairs in the field of view and dividing this amount by the total leaf area measured within the field of view. Leaf trichome counts were performed on a total of 155 C, 271 H, and 23 V plants in 2004 and 193 C, 210 H, and 50 V plants in 2005.

Population data and interpretation

Short-term climatic effects on populations

Short-term climatic variation (Fig. 2) existed at C, V, and H sites. To determine whether climatic variation affects leaf morphology, we used a stepwise discriminant analysis (PROC STEPDISC: SAS 2002) to test which specific months of the year between the beginning of the growing season (April) and population sampling (July) had significant effects on this parameter. Separate general linear models were performed on both total annual water availability and each year's deviation from 30-year average water availability (monthly value − 30-year average) for the months of April–July (PROC GLM: SAS 2002).

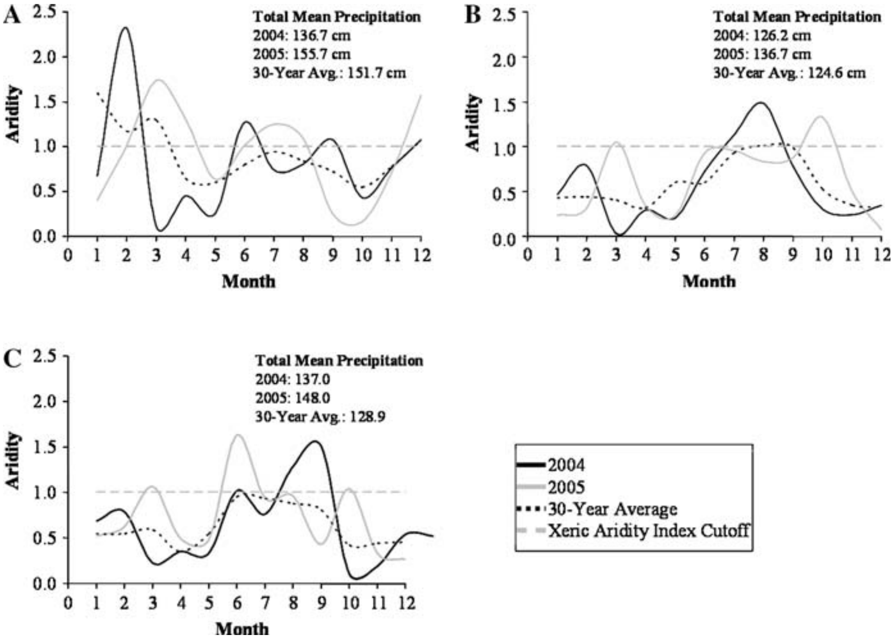


Fig. 2 Mean monthly (1–12) aridity (ratio of precipitation to potential evapotranspiration) for populations of plants within *Piriqueta caroliniana* complex including (**a**) *carolinianas*, (**b**) *viridis*, and (**c**) *hybrid* throughout Florida for the 30-year average and 2004–2005 growing seasons. An aridity value <1 indicates water stress

Each model accounted for variation due to year (2004 and 2005) and morphotype (C, V, or H).

Between year effects on populations

To determine whether differences between years had an effect on leaf morphology, separate general linear models were performed on leaf traits including leaf area, width/length ratio, and trichome density (PROC GLM: SAS 2002). Each model accounted for year and between-site variation in leaf morphology in the different morphotypes (C, V, and H) examined in this study. Values were log or square root transformed when necessary to approximate normality for residuals (Sokal and Rohlf 1995).

Results

Yearly aridity differed between the 2004 and 2005 seasons. Overall, 2005 had significantly greater aridity than the 2004 season ($F = 66.34, P < 0.0001, \mathrm{df} = 1, 28$). Yearly aridity varied among taxa as well. A post hoc analysis using Tukey multiple range tests of the pooled 2004 and 2005 data indicated overall aridity for C populations was significantly greater than H ($P < 0.05$), although V populations did not have significantly greater aridity than H populations.

Monthly 30-year aridity averages only differed between taxa for the months of June and July. H had significantly greater aridity ($P < 0.05$) than C and V during the month of June, and V had significantly greater aridity ($P < 0.05$) during the month of July. Monthly, between-year aridity, 2004 versus 2005, also differed for C, V, and H morphotypes (Table 1).

Trait means of the leaves that were collected in July 2004 and 2005 (therefore representing climatic conditions of June 2004 and 2005) differed between years (Table 2). Leaf characters that were significantly different between years included width/length ratio ($F = 21.88, P < 0.0001, \mathrm{df} = 1, 902$) and leaf hair density ($F = 39.28, P < 0.0001, \mathrm{df} = 1, 902$). Leaf width/length ratio and leaf hair density increased between 2004 and 2005. Leaf area, however, was not significantly different between 2004 and 2005 ($F = 0.20, P = 0.6561, \mathrm{df} = 1, 902$). Although leaf length did not differ significantly between 2004 and 2005, leaves were longer (Mean leaf length = 3.79 cm) in 2004 when compared to 2005 (Mean leaf length = 3.47 cm). Each morphotype's leaf trait variation was similar to the overall variation mentioned previously, and hybrid leaf characters were intermediate between C and V leaves for leaf area and width/length ratio, and transgressive for hair density ($F = 3299.66, P < 0.0001, \mathrm{df} = 2, 901$; Table 2 and Fig. 3).

Correlations between 2004 and 2005 leaf trait values and monthly (April–July) and total 30-year average, 2004, and 2005 aridity values were generally moderate ($R^2 < 0.50$). The strongest correlations for

Table 2 Percent change in leaf traits (+ or −), including leaf hairs/area, width/length ratio, and area, between the 2004 and 2005 growing seasons for C (*caroliniana*), V (*viridis*), and H (hybrid) plants within the *Piriqueta caroliniana* complex

Taxa	Leaf hairs/ Area	Leaf width/ Length ratio	Leaf area
C	(+)86.72%*	(+)2.87%*	(−)7.6%^{NS}
V	0.00%$^{+, NS}$	(+)44.84%	(+)58.28%^{NS}
H	(−)5.09%*	(+)19.99%*	(+)1.16%^{NS}

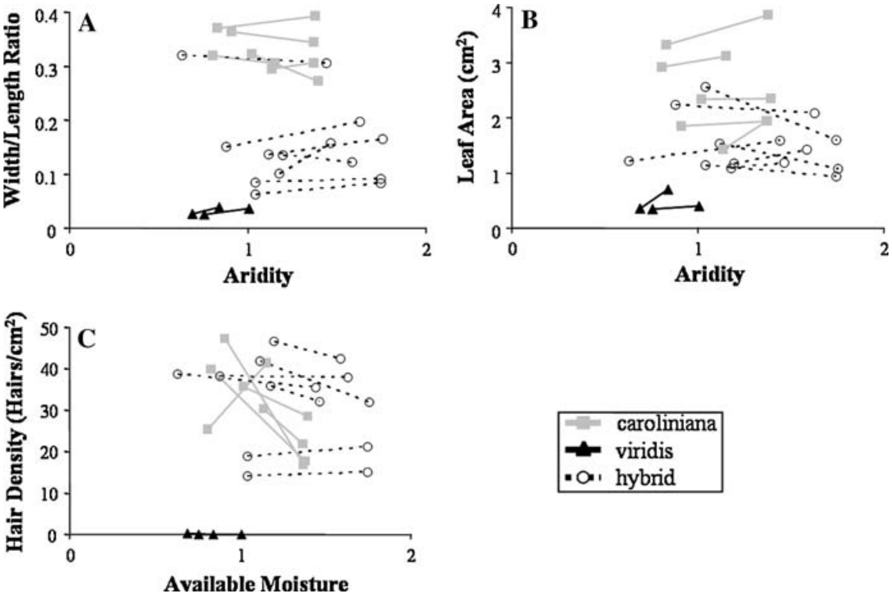
* Indicates that leaf traits were significantly different ($P < 0.05$) between 2004 and 2005. ^{NS}: Indicates that leaf traits were not significantly different ($P > 0.05$ between 2004 and 2005. $^{+}$: V plants exhibited increased hair density between 2004 and 2005, however this increase is negligible (Mean 2004 hair density = 0.00 hairs/cm^2 and Mean 2005 hair density = 0.06 hairs/cm^2)

Table 1 Percent change in aridity (+ or −) between the 2004 and 2005 growing seasons

Taxa	C	V	H
April 2004 vs. 2005 % difference	(+)211.75%^{A,D}	(+)17.08%^{B,E}	(+)40.11%^{B,E}
May 2004 vs. 2005 % difference	(+)161.17%^{A,D}	(+)15.42%^{B,D}	(+)59.78%^{A,D}
June 2004 vs. 2005 % difference	(−)14.85%^{A,D}	(+)27.41%^{B,D}	(+)65.99%^{B,D}
July 2004 vs. 2005 % difference	(+)70.73%^{A,D}	(−)15.6%^{A,D}	(+)24.12%^{A,D}
Growing season total 2004 vs. 2005 % difference	(+)55.37%^{A,D}	(+)45.36%^{B,D}	(+)4.34%^{A,D}

Different superscript letters indicate statistically significant ($P < .05$) differences between 2004 (A or B) and 2005 (D or E)

Fig. 3 Variation of mean aridity (ratio of precipitation to potential evapotranspiration) and *Piriqueta caroliniana* complex leaf characters including (**a**) width/length ratio, (**b**) leaf area, and (**c**) hair density for *caroliniana, viridis,* and hybrid plants measured at natural field populations in Florida and southern Georgia. Each line represents a separate natural population, and the slope of that line is directly related to the change in leaf characters and aridity between 2004 and 2005



2004 leaf traits were between width/length ratio and April 30-year average ($R = +0.82$, $P = 0.0005$) aridity and leaf hair density and July aridity ($R = -0.81$, $P = 0.0004$). In 2005 strong correlations were found between leaf width/length ratio and 30-year average April aridity ($R = +\ 0.80$, $P = 0.0006$), leaf width/length ratio and April aridity ($R = +0.78$, $P = 0.001$), leaf width/length ratio and total aridity ($R = +0.74$, $P = 0.0023$), leaf area and April aridity ($R = +0.71$, $P = 0.0043$), leaf hair density and May aridity ($R^2 = +0.73$, $P = 0.0032$), and leaf hair density and total aridity ($R = +\ 0.77$, $P = 0.0014$).

Discussion

Environmental heterogeneity has apparently influenced the distribution and morphology of *caroliniana*, *viridis*, and hybrids in the *Piriqueta caroliniana* complex. Populations of morphotypes and hybrids within this complex that were sampled in 2004 and 2005 exhibited differences in yearly water availability and mean leaf traits. These results support the hypothesis that conditions of the physical environment influence the leaf morphology of plants. The range of leaf morphological diversity among hybrid populations is of particular interest since it presumably represents the outcome of past selection on recombinant hybrid genotypes at each site. These data support the hypothesis that leaf traits and plasticity responses toward narrower shape and higher trichome density are associated with increased drought conditions.

Environmental heterogeneity

Monthly and yearly variation in water availability among the regions occupied by the C, H, and V populations suggests that water availability may be more limiting for some populations of *Piriqueta caroliniana* complex than others. Overall, water availability was lower for H populations than for the C parental populations. If H plants have higher fitness under drought conditions when compared with C plants, this could help explain the displacement of the C morphotype and the historical northward expansion of the hybrid zone through dry central Florida (Martin and Cruzan 1999). This is consistent with the view that novel environments, in which parental plants exhibit lower fitness, can provide an opportunity for hybrid success (Anderson 1949; Cruzan and Arnold 1993; Graham et al. 1995). Hybrids may have developed novel adaptations to tolerate and succeed in the more extreme drought conditions present in central Florida. Over time this may have fostered hybrid superiority over the C morphotype in central Florida and may have contributed to the displacement of that morphotype, which historically occupied this region (Maskas and Cruzan 2000).

Leaf traits

We found that mean leaf shapes were significantly narrower during the drier growing season of 2004 compared to the wetter 2005 season. This trend remained consistent when each morphotype was examined separately. Decreasing leaf width/length ratio may allow plants in the *Piriqueta caroliniana* complex to reduce the effects of heat loading by increasing the effectiveness of convective cooling, thereby diminishing overall water loss to the environment (reviewed in Givnish 1987). It was expected that overall leaf area would decrease, because in water-stressed ecosystems, plants often exhibit a reduction in leaf area (Parkhurst and Loucks 1972; Thuiller et al. 2004). However, we did not find that overall leaf area changed between the 2004 and 2005 seasons. These *Piriqueta* morphotypes appear to be maximizing their photosynthetic area by decreasing leaf width while simultaneously increasing leaf length (Picotte et al. 2007). This strategy may be advantageous under hot conditions and unpredictable rainfall because it maximizes photosynthetic area while increasing the efficiency of convective cooling and heat loss to the environment. It is also possible that plants in the *Piriqueta caroliniana* complex have some developmental constraint on leaf size so that leaf length is negatively correlated with leaf width. In either case, leaf shape plasticity allows plants to overcome water and heat stress, and maximize their growth potential in hot and periodically arid environments (reviewed in Gibson 1998).

Another way in which water and heat stress can be alleviated is through the alteration of leaf trichome densities (Nobel 1999). The mean leaf hair density in populations of the C morphotype increased in 2005 season during the drier month of June, indicating that fewer hairs are produced during wetter climatic conditions. Having higher densities of leaf hairs in June 2005 may have decreased water loss in two ways. Plants that have higher leaf hair densities have been found under some circumstances to have higher leaf reflectance (Ehleringer 1976; Ehleringer and Mooney 1978; Ehleringer and Werk 1986). Increasing leaf reflectance would decrease the overall leaf temperature by decreasing heat loading. However, in *Piriqueta* there does not appear to be a correlation between trichome density and reflectance (Picotte et al. 2007). Higher leaf hair density could also increase the leaf boundary layer (i.e., a thin layer of stagnant air adjacent to the surface of the leaf reviewed in Schuepp 1993), and trichome density has been shown to increase water use efficiency under drought conditions in *Piriqueta caroliniana* (Picotte et al. 2007).

Previous studies have documented that hybrid plants can exhibit intermediate or extreme morphological characters (transgressive traits; Rieseberg 1995). In this study we found that hybrid morphology was often intermediate for traits such as leaf area and length/width ratio, but hybrids sometimes exhibited higher leaf hair densities than parental morphotypes during the dry 2004 season, suggesting this trait can be transgressive. Similar results were found in previous studies of *Piriqueta* by Martin and Cruzan (1999) and Picotte et al. (2007). Both intermediate leaf shape and higher trichome density could allow the hybrid derivative H genotypes to tolerate the drier conditions present in their habitats. The hybrids' tolerance of a greater range of water availability in comparison with the parental morphotypes could help explain the northward advance of the hybrid zone.

Although V morphotype plants do occasionally have hairs (Mean hair density = 0.06 hairs/cm^2), their low hair density probably does not reduce water loss to the environment by increasing the leaf boundary layer. Instead the glabrous V leaves are much narrower and longer then both the C and H genotypes, which should allow the V plant to reduce heat-loading and subsequent water loss (reviewed in Givnish 1987). Although we did not measure soil moisture during the experiment, we did note that populations experienced sporadic flooding. Previous experiments have determined that the V morphotype and hybrids produces aerenchyma when subjected to flooding, are more fit under flooded conditions than the C morphotype (Benz et al. 2007). V's glabrous leaves should also allow for greater CO_2 diffusion between the atmosphere and the plant, thereby increasing photosynthesis when the plant is not under drought stress (reviewed in Nobel 1999). Overall, V's adaptations allow it to tolerate both periodic flooding (which is uncommon in C populations) and drought.

Adaptation and plasticity in contrasting environments

Alteration of phenotypic traits in response to the physical environment is generally viewed as a response to selection and adaptation to the prevailing local conditions, which may ultimately result in ecological speciation (Schlichting and Pigliucci 1998; Schluter 2000). Few studies, however, have measured the phenotypic plasticity of natural plant populations (see Noel et al. 2007 for a notable exception). It is striking that plants of the C morphotypes had substantially greater changes in their leaf hair density compared to the H derivatives. In temporally variable environments, the ability of perennial plants to respond appropriately to seasonal climatic changes can be important component of adaptation (for reviews Pigliucci 2001; Sultan 1987; van Kleunen and Fischer 2005). However, over time in a stressful environment, traits that are under constant selection may become canalized (Ghalambor et al. 2007). In this scenario plants that can tolerate fluctuating environmental stressors, such as water availability, with consistent phenotypic expression would outcompete more plastic plants that use more energy in their morphological responses to stress (DeWitt et al. 1998). Greater energy expenditure coupled with the time lag between the environmental change and plant response, could select against highly plastic plants. The hybrids' lack of plasticity combined with their observed tolerance of variable environmental conditions lends credence to the argument that plasticity can be costly and may not always be favored by selection (reviewed in van Kleunen and Fischer 2005).

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