

Genetic variation in photosynthetic characteristics among invasive and native populations of reed canarygrass (*Phalaris arundinacea*)

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Abstract With the extensive spread of invasive species throughout North America and Europe there is an urgent need to better understand the morphological and physiological characteristics of successful invasive plants and the evolutionary mechanisms that allow introduced species to become invasive. Most ecological studies have focused on morphological differences and changes in community dynamics, and physiological studies have typically explored the differences between native and invasive species. In this study, 15 different genotypes of *Phalaris arundinacea* from both its native (European) and invasive (North American) range were grown in a common garden experiment to monitor the physiological differences between native and invasive genotypes. Here we present data that suggests high variability exists in the physiological traits among genotypes of *P. arundinacea*, yet genotypes from the native range are not necessarily physiologically inferior to the hybridized invasive genotypes. Previous work has shown that multiple introductions of *P. arundinacea*

from various European locations to the United States resulted in numerous hybridization events, yielding more genetic variability and phenotypic plasticity in the invasive range. Of the genotypes studied, both morphological and physiological traits of genotypes with French origin were significantly different from the plants from the Czech Republic, North Carolina, and Vermont. The lack of clear differences between native and invasive genotypes indicates that physiological traits may be highly conserved in *P. arundinacea* and enhanced photosynthetic rates are not indicative of successful invasive genotypes. Instead, morphological traits and defensive secondary compound metabolism may play a more important role in the success of *P. arundinacea* within its invasive range, and patterns of genetic variation in physiological traits between invasive and native range may be more important than the mean traits of each region when explaining reed canarygrass' invasive potential in North America.

Keywords *Phalaris arundinacea* · Genotype · Invasive · Native · Physiology · Photosynthesis · Morphology

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Introduction

Over the past decade, evidence has accumulated that introduced species can rapidly evolve a high invasive ability following their introduction into a new region

(e.g. Bohn et al. 2004; Huey et al. 2000; Lavergne and Molofsky 2007; Maron 2006); and this has shed new light on the mechanisms that can turn introduced species into invasive ones (Callaway and Maron 2006; Mack 1995; Lambrinos 2004; Stockwell et al. 2003). Shifts in a number of biological features have been documented in invasive plant populations relative to their native conspecifics, including growth rate, anti-herbivore defenses, reproductive ability and mating systems (Amsellem et al. 2001; Blair and Wolfe 2004; Brown and Eckert 2005; DeWalt et al. 2004; Lafuma and Maurice 2007; Lavergne and Molofsky 2007; Maron et al. 2004; Siemann and Rogers 2001). However, differences in physiological traits have not been fully investigated between invasive and native populations of a single introduced plant species.

There is considerable evidence that photosynthetic traits and physiological response to abiotic factors can influence a species' ecological distribution along environmental gradients (Baskauf and Eickmeier 1994; Chapin and Oechel 1983; Körner and Diemer 1987; Mooney and Billings 1961; Reich et al. 1999; Reich et al. 1997). Mean photosynthetic rate and biomass allocation to leaves has been shown to influence a plant's ability to assimilate carbon and thus contribute to its overall growth rate (Dijkstra and Lambers 1989; Poorter and Garnier 1999), which is an important adaptation in habitats where high competition for resources is present (Grime 1977; Grime and Hunt 1975). Invasive plants have also been shown to have higher photosynthetic rates and longer sustained photosynthetic activity when compared to noninvasive, native species (McDowell 2002). Previous studies have documented that some invasive species can have higher maximum photosynthetic rates (A_{\max}) or higher water use efficiency (WUE) than non-invasive congeners (McDowell 2002), and that invasive plants can have higher relative allocation to leaves than non-invasive congener species (Feng et al. 2007). In low-resource systems where nutrients and water are limited, invasive plants have also been shown to have higher resource efficiency than native plants (Funk and Vitousek 2007). Therefore, a shift in traits related to resource acquisition or photosynthetic response to abiotic factors may directly influence species adaptations in areas of range expansion as well as a species ability to invade new habitats. While these differences may favor invasive species over co-occurring native species for resource competition, it is not clear whether particular suites of

physiological traits have contributed to the invasive ability of introduced species. This would require that introduced populations exhibit a substantial evolvability (i.e. genetic variance) for a number of photosynthetic features in order to respond to potential new selective pressures operating on photosynthetic parameters. For example, Heschel et al. (2004) found variation in the WUE of an understory herbaceous plant between xeric and mesic locations, and higher WUE was indicative of successful adaptation to a variety of moisture conditions. Interspecific variation in photosynthetic response to abiotic variables such as light and ambient CO_2 may be critical for introduced populations to adapt to varied light environments (e.g. understory versus open habitats) and to future increases in atmospheric CO_2 . Phenotypic plasticity for photosynthetic traits between genotypes has been recognized for some time, and that flexibility in photosynthetic capacity is a strong determinant of successful establishment and colonization of new areas (Arntz and Delph 2004; Zangerl and Bazzaz 1983). Benowicz et al. (2000) has shown for two different hardwood tree species that physiological properties between intraspecific populations varies depending on the abiotic variables of geographic locations, and such studies can help predict changes in population growth or distribution in response to climate change (Benowicz et al. 2000).

In this study, we investigate the photosynthetic characteristics of native and invasive genotypes of reed canarygrass (*Phalaris arundinacea* L., Poaceae), a C_3 perennial grass that is invasive to North American wet habitats (Lavergne and Molofsky 2004). It was recently demonstrated that the species' invasiveness resulted from multiple introductions of European strains that have recombined allowing for natural selection for genotypes with high rates of vegetative colonization (Lavergne and Molofsky 2007). Here we test how photosynthetic characteristics, as well as morphological traits related to resource acquisition, vary between native and invasive populations of reed canarygrass.

Material and methods

Genotype choice

We selected 16 genotypes from the 90 previously studied genotypes selected by Lavergne and Molofsky (2007). To increase our ability to distinguish

differences between genotypes, we selected the two tallest and shortest genotypes (among the original 90 studied); the remaining 12 genotypes were randomly selected so that there were four genotypes from each of the four regions (Czech Republic, France, North Carolina, and Vermont) for a total of 16 genotypes. One genotype from the Czech Republic failed to propagate, leaving 15 genotypes.

Growth and physiological experiment

Propagation of plants

We propagated the genotypes from cuttings of adult plants by covering the stem nodes in Hormodin I rooting hormone (OHP, Inc., Mainland, PA, USA), and then placed the stems in flat plastic trays covered with 3 cm of Fafard 3B soil (Conrad Fafard, Inc. Agawam, MA, USA). The trays were watered twice daily, and fertilized twice per week with 300 ml half strength Hoagland's solution (Hoagland 1941). This treatment allowed for ramets to begin growing from the original stem nodes, thus producing genetically identical plants. After 6 weeks (12/2/2004), the ramets were cut just above the first leaf, and all but 1.5 cm of root tissue was cut, creating four identical replicates for each genotype totaling 60 plants. These plants were then transplanted into plastic pots with a 1:1:1 mixture of coarse vermiculite, coarse sand, and fine sand. Each pot received the same watering and fertilization schedule as described above. The plants were randomly positioned on a greenhouse on two benches (1.2 × 6.4 m). Plants were placed under high-pressure sodium lamps, receiving 1,200 $\mu\text{mol m}^{-2} \text{s}^{-2}$ Photosynthetic Photon Flux Density (PPFD) for 12 h each day with a daytime temperature of 18–21°C and a nighttime temperature of 13–16°C.

Physiological and morphological measurements

Plants were measured weekly for total height from soil surface and total shoot number. Approximately 90 days after transplanting, physiological measurements were conducted between 1,000 and 1,300 h to eliminate any photoperiod effects or afternoon drying. All plants were watered prior to physiological measurements. Instantaneous photosynthetic measurements were made on all

60 plants on the leaf at the third node of each plant using a LI-COR 6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA). Photosynthetic light response (0, 250, 500, 750, 1,000, 1,500, 2,000, and 2,500 $\mu\text{mol m}^{-2} \text{s}^{-2}$ PPFD at 400 ppm CO_2) and CO_2 response curves (100–600 ppm in 100 ppm increments at 1,200 $\mu\text{mol m}^{-2} \text{s}^{-2}$ PPFD) were generated for one representative plant from each genotype using the same LI-COR 6400. Light was provided by the LI-6400-02B LED light source. The leaf tissue within the chamber head after measurements were complete were clipped and dried in a drying oven at 80°C for 48 h. The leaf samples were then weighed and used to calculate photosynthesis per unit of leaf mass.

Once physiological measurements were complete, plants were harvested and dry weight was measured. Leaves, stems, and roots were disassembled and placed in a drying oven for 80°C for 48 h. The plant material was then removed and weighed to assess leaf mass, stem mass, root mass, total biomass, leaf mass ratio (total leaf mass/total biomass), and root/shoot biomass ratio.

Statistical analyses

Leaf gas exchange, morphological characteristics, and biomass allocation patterns were analyzed using linear mixed effect models (Pinheiro and Bates 2000), with “genotype” or “clone nested within genotype” as random effects. Two types of fixed effects were fit in two separate models: a “range” effect to test for possible trait variation between genotypes of different original range (invasive versus native), and a “location” effect to test for possible variation between genotypes of different locations (Czech Republic, France, Vermont, North Carolina), irrespective of their range of origin. The significance of each fixed effect was quantified by computing the change in model's Akaike Information caused by the effect (Burnham and Anderson 2002), and by performing a log-likelihood ratio test (Venables and Ripley 2002).

Photosynthetic response to ambient CO_2 and incident light were analyzed by fitting linear and non-linear mixed effect models, respectively (Pinheiro and Bates 2000), with genotype as a random effect and an autoregressive correlation structure to account for repeated measurements. Photosynthetic rate (A) was fit as function of ambient CO_2 with the linear equation $A = b + a \times [\text{CO}_2]$ to compute the following two

parameters: photosynthetic CO₂ efficiency (A_c) and CO₂ compensation point (CCP). A_c was estimated as the slope (a) of photosynthetic increment as a function of ambient CO₂. CCP was estimated as $-b/a$ and corresponds to the CO₂ compensation point. Photosynthetic rate was fit as a function of incident light by using a Mitscherlich function (Potvin et al. 1990) of the form $A_{\max}(1 - e^{-A_q(\text{PPFD}-\text{LCP})})$, with PPFD (photosynthetic photon flux density), LCP (light compensation point), A_q (photosynthetic quantum efficiency), and A_{\max} (maximum photosynthetic rate). The Mitscherlich function, which often fits the data better than classic models such as non-rectangular hyperbola (Farquhar and Sharkey 1982), is becoming the widely accepted method of light curve fitting in physiological ecology (Peek et al. 2002). Finally, we tested whether these parameters of photosynthetic responses (A_c , CCP, A_{\max} , A_q and LCP) varied between genotypes of different range or location of origin by performing a likelihood ratio test (Venables and Ripley 2002).

We also quantified genetic variance in traits of leaf gas exchange, morphological characteristics, biomass allocation, and parameters of photosynthetic response curves by computing the coefficient of genetic variation for each trait, as the square root of the genetic variance divided by the trait mean (Houle

1992). This metric of evolvability is more appropriate than heritability in our case (although both metrics are related), as we wanted to compare evolvability between traits that may have very different residual variances (as traits are measured with different protocols and with varied level of data nestedness). Evolvability was computed separately for each range by extracting intra-population genetic variance and using variance partitioning with population nested within location as random effect. Variance components were estimated and restricted maximum likelihood and confidence intervals of coefficients of genetic variation were obtained by jackknifing over genotypes (Bonnin et al. 1996; Roff 1997).

Results

Leaf gas exchange, morphology, biomass allocation

Maximum instantaneous photosynthetic rates varied between 0.25 and 4.16 mmol g⁻¹ s⁻¹ across all genotypes, with the most variance among the FR genotypes (Fig. 2). There was no significant effect (at the 5% level) of range on physiological traits

Table 1 Variation in leaf-gas exchange and morphological characteristics between ranges of study genotypes (invasive, native) and locations of study genotypes (Czech Republic, France, North Carolina, Vermont)

	Range effect			Location effect		
	ΔAICc	LogLik	LogLik ratio test	ΔAICc	LogLik	LogLik ratio test
Photosynthetic rate	1.32	100.8	3.46 ₁ [†]	1.38	116.3	8.03 ₃ [*]
Stomatal conductance	0.58	861.8	2.72 ₁ [†]	2.25	909.1	8.90 ₃ [*]
Internal CO ₂ concentration	-0.33	-671.2	1.81 ₁ ^{ns}	1.73	-664	8.38 ₃ [*]
Transpiration	0.55	337.1	2.70 ₁ ^{ns}	0.54	343.7	7.19 ₃ [†]
Water use efficiency	-1.62	-88.4	0.52 ₁ ^{ns}	-5.2	-71.4	1.45 ₃ ^{ns}
Stem height	-1.87	-240.4	0.52 ₁ ^{ns}	-7.33	-239.5	0.73 ₃ ^{ns}
Shoot number	-1.65	-181.1	0.75 ₁ ^{ns}	0.61	-176.3	7.49 ₃ [†]
Total leaf mass	-1.43	-122.8	0.96 ₁ ^{ns}	0.84	-123.2	8.91 ₃ [*]
Leaf mass ratio	-2.35	139.8	0.04 ₁ ^{ns}	-7.3	140.2	0.76 ₃ ^{ns}
Root:Shoot biomass ratio	-2.04	51.1	0.35 ₁ ^{ns}	-5.77	53.9	2.29 ₃ ^{ns}
Total biomass	-1.61	-205.5	0.78 ₁ ^{ns}	0.44	-205.7	8.10 ₃ [*]

All models are linear mixed effects models with range or location of genotypes as fixed effects, genotype as a random effect, and distinct variance parameters for each range or location. Variation in model AICc (corrected Akaike Information Criterion) caused by fixed effects and model's log-likelihood are given in columns ΔAICc and LogLik, respectively. Significance of fixed effects was assessed using a likelihood ratio test, comparing the likelihood ratio to a χ^2 distribution with appropriate degrees of freedom (subscript number)

[†] $P < 0.1$, * $P < 0.05$, ns non significant

(Table 1, left column). However, a location had significant effect on both physiological and morphological traits (Table 1, right column). Generally, FR genotypes had higher leaf photosynthetic rates (A) and stomatal conductance (g_s) relative to the other three locations, which never showed significant differences between them. The FR genotypes typically had fewer shoots and lower leaf biomass than CZ, NC and VT genotypes (Fig. 1d, e).

Photosynthetic response to CO₂ and light

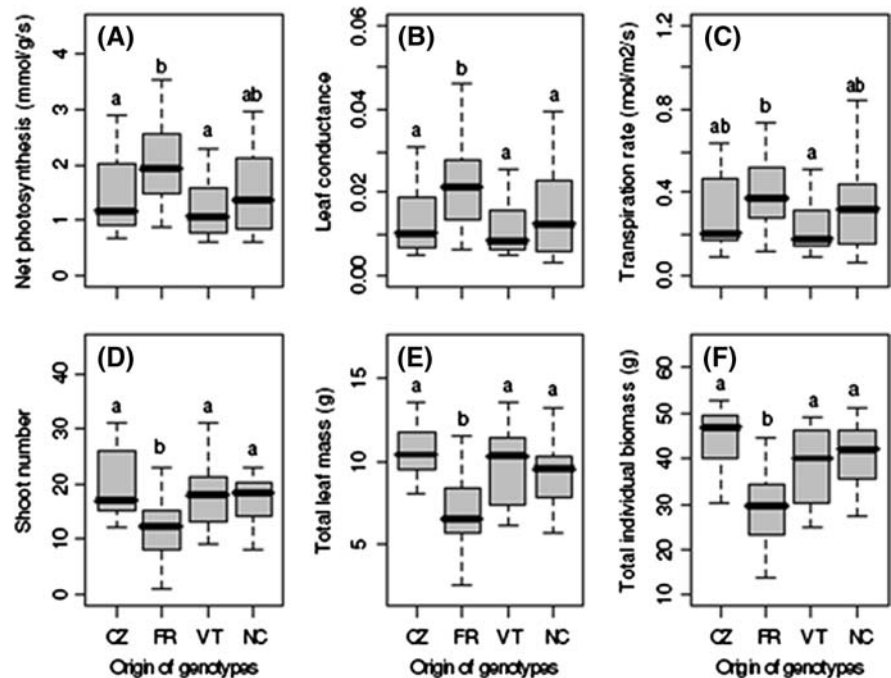
Photosynthetic response to increasing ambient CO₂ levels increased linearly in all individuals sampled; yet there were no distinct groupings based on range or location. Mean CO₂ compensation point was similar for all locations, with the most variance in the VT genotypes and the least variance in the NC genotypes. Variance in the slope of the CO₂ response curves was lowest in the CZ plants, while considerable variance was evident among the other locations (Fig. 2a).

Three groups of plants separated based on light response curve; one group became light saturated at a low light intensity (approximately 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$) with high relative photosynthetic rates (a mix of CZ,

FR, NC and VT genotypes), the second group also saturated at a low light intensity with low relative photosynthetic rates, and the third group composed of two FR genotypes never reached a light saturation point and also showed the highest rates of photosynthesis of all the genotypes (Fig. 2b). These groups however, were independent of range or location. FR genotypes differed significantly from the other locations in light compensation point, quantum efficiency, and maximum rate of photosynthesis, which is consistent with the instantaneous photosynthesis measurements. The FR genotypes also had the highest variance in each of those physiological parameters (Fig. 2).

No general differences were found to be significant following likelihood ratio tests (Table 2), since most of the variation was observed for different parameters of photosynthetic response curves between genotypes within each location (Fig. 3). Some parameters were significantly different between FR and CZ genotypes following a posteriori contrasts: CO₂ photosynthetic efficiency A_c ($P = 0.04144$, Fig. 2a, inserted boxplot), light compensation point (LCP) ($P = 0.044567$, Fig. 2b inserted boxplot) and max photosynthetic rate (A_{max}) ($P = 0.05014$, Fig. 2b).

Fig. 1 Leaf photosynthetic rate (a), leaf conductance (b), leaf transpiration rate (c), shoot number (d), total leaf mass (e) and total individual biomass (f) of reed canarygrass genotypes as a function of their geographic origin. Locations of origin are Czech Republic (CZ) and France (FR) for the native range of the species, and Vermont (VT) and North Carolina (NC) for the invasive range of the species. Letters indicate groups that were significantly different following a posteriori contrasts analyses (5% level)



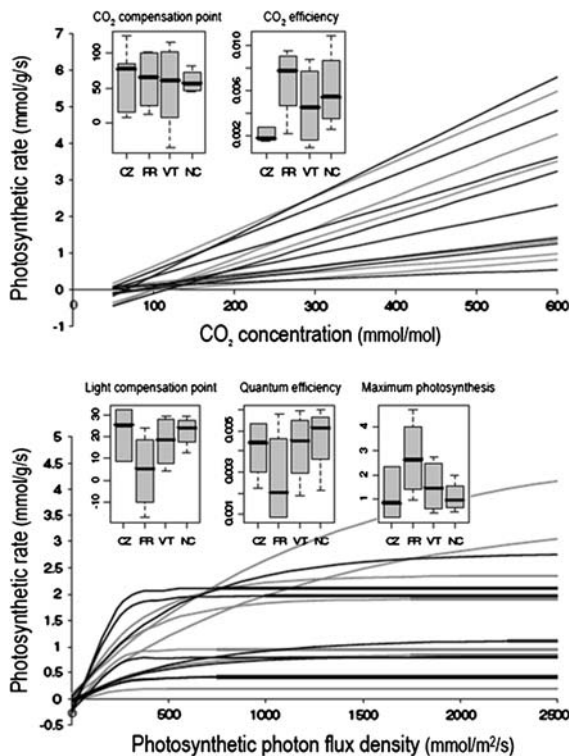


Fig. 2 Photosynthetic response of invasive genotypes (black lines) and native genotypes (grey lines) to variation in ambient CO₂ (a) and light intensity (b). Models of photosynthetic responses were fitted separately for each genotype, and genetic variation in different response parameters was then analyzed relative to genotype origins (inserted boxplots). Genotype origins are Czech Republic (CZ) and France (FR) for the native range of the species, and Vermont (VT) and North Carolina (NC) for the invasive range of the species. Photosynthetic response of each genotype as a function of CO₂ concentration was fitted with a linear model, to compute CO₂ compensation point (CO₂ concentration where photosynthesis becomes greater than respiration) and photosynthetic CO₂ efficiency (slope of photosynthetic increment). Genotypes' photosynthetic response were fitted using a Mitscherlich function of the form $A_{\max}(1 - e^{-A_q(\text{PPFD} - \text{LCP})})$, with PPFD being the photosynthetic photons flux density, LCP being the light compensation point (light threshold for which carbon acquisition becomes positive), A_q being the photosynthetic quantum efficiency (initial slope of photosynthetic increment) and A_{\max} being the maximum photosynthetic capacity at light saturation (final threshold value)

Genetic variance in phenotypic traits

Coefficients of genetic variation were significantly different from zero for all traits. Morphological and leaf gas-exchange traits had a low coefficient of genetic variation, generally lower than 35% (Fig. 3).

However, both invasive and native populations exhibited relatively high coefficient of genetic variation for all parameters of light and CO₂ response curves (Fig. 3).

Several photosynthetic traits exhibited higher genetic variance within native populations relative to invasive ones, including A , g_s , and transpiration rate (Fig. 3). Conversely, root/shoot biomass ratio, and parameters of CO₂ response curve (carbon compensation point and CO₂ efficiency) exhibited higher genetic variation within invasive populations relative to native ones.

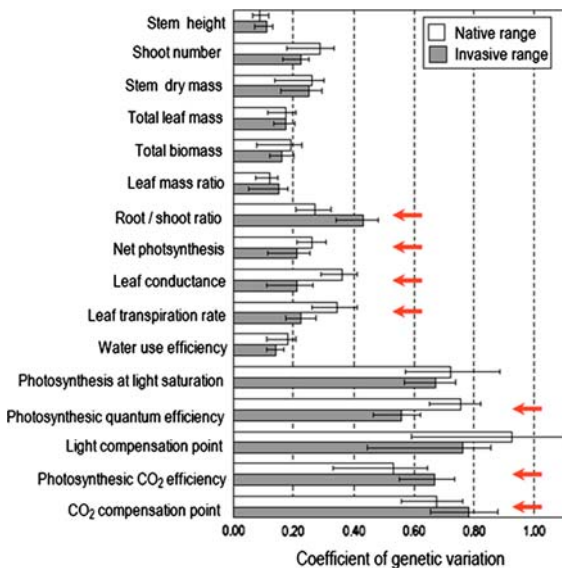
Discussion

Of the physiological and morphological traits observed, only photosynthetic rate (A) and stomatal conductance (g_s) were significantly different between native and invasive genotypes (Table 1 and Figs. 1 and 3). The higher rates of A and g_s observed in the native range were due to two FR genotypes. Moreover, FR genotypes showed a high level of variance among individual plants as well as significantly higher A , A_{\max} , g_s , and lower shoot number, total leaf mass, and total biomass than the genotypes from the other three locations. These data suggest that the FR genotypes were significantly different in physiological and morphological characteristics from the CZ, NC, and VT genotypes yet no distinct pattern was observed between native and invasive genotypes. With respect to the light response curves, there were no significant differences for range or location, yet the FR genotypes again showed a high degree of variability among individuals, with two genotypes reaching high individual rates of photosynthesis and never becoming light saturated (Tables 1 and 2, Fig. 3). Meanwhile, the invasive (NC and VT) and CZ genotypes appeared to respond with a more aggressive vegetative strategy, with vigorous shoot production and spatial spread at the expense of high photosynthetic rates at each stem. Higher photosynthetic efficiency would allow the species to take advantage of short-term favorable windows of high light, such as accidental canopy opening following disturbances, and also allow for rapid growth rate in highly competitive environments. WUE was not found to be significantly different between locations or ranges, but this may have been due to the favorable

Table 2 Variation in parameters of photosynthetic response to ambient CO₂ and incident light between ranges of study genotypes (invasive, native) and locations of study genotypes (Czech Republic, France, North Carolina, Vermont)

		Range effect			Location effect		
		ΔAICc	LogLik	LogLik ratio test	ΔAICc	LogLik	LogLik ratio test
CO ₂ response curve	CCP	-2.38	-175.6	0.15 ₁ ^{ns}	-8.76	-161.03	0.25 ₃ ^{ns}
	A _c	-2.43	51.72	0.11 ₁ ^{ns}	-3.48	68.7	5.45 ₃ ^{ns}
Light response curve	LCP	-1.78	33.6	0.76 ₁ ^{ns}	-3.92	39.05	5.01 ₃ ^{ns}
	A _q	-0.78	284.9	1.77 ₁ ^{ns}	-5.83	299.2	3.09 ₃ ^{ns}
	A _{max}	-2.05	69.34	0.49 ₁ ^{ns}	-4.47	74.82	4.45 ₃ ^{ns}

Variation in model AICc (corrected Akaike Information Criterion) caused by range or location effects and model's log-likelihood are given in columns ΔAICc and LogLik, respectively. Significance of fixed effects was assessed using a likelihood ratio test, comparing the likelihood ratio to a χ^2 distribution with appropriate degrees of freedom (subscript number). LCP = light compensation point, A_q = photosynthetic quantum efficiency, A_{max} = maximum photosynthetic capacity (at light saturation), A_c = photosynthetic CO₂ efficiency, CCP = CO₂ compensation point

**Fig. 3** Coefficients of genetic variation for morphological traits, measurements of leaf-gas exchanges and parameters of light and CO₂ response curves. Red arrows correspond to statistically significant differences ($P < 0.05$)

growth conditions which allowed for very little water stress for the plants.

The morphological and physiological differences between native and invasive genotypes were negligible, suggesting that the physiological differences are not responsible for aiding in invasiveness. It appears as though the CZ, NC, and VT genotypes have similar physiological traits, while the FR genotypes were generally significantly different. Notably, a phylogenetic tree of 12 different populations of *P. arundinacea* (Lavergne and Molofsky unpublished

data) shows that CZ, NC, and VT genotypes are closely related and the FR genotypes fall into a separate clade. The results from this study and the phylogenetic study suggest that physiological traits may be highly conserved and less susceptible to changes due to hybridization. The habitat that the FR genotypes were taken from is highly competitive, with a high species diversity and intense interspecific competition for light, nutrients, and space. Thus, the FR genotypes may be adapted toward a more compact morphology (lower shoot number and shorter height) and efficient physiology (higher photosynthetic rate and lower light compensation point). Several Mediterranean species have been shown to exhibit slower growth rates and high secondary compound metabolism, which is thought to be the result of high herbivore and ungulate grazing pressure (Massei et al. 2000; Cruz et al. 2003).

Allocation of assimilated carbon to leaves and stems is an important trait allowing for the ability to compete for light and space, and this process is thought to be highly competitive in *P. arundinacea* in North America and France (Lavergne and Molofsky 2004, 2006). Also, high genetic variance in root/shoot ratio (consistent with Lavergne and Molofsky 2007) suggests that this species is able to rapidly adapt to a wide range of above- and belowground competition (Table 1 and Fig. 1).

The FR genotypes seem to have adapted toward higher photosynthetic rates, yet the gain in assimilated carbon does not appear to be allocated to increases in biomass (Fig. 2). The disconnect

between acquisition and allocation could be due to the greater production of secondary compounds present in the leaves. It has been proposed that within introduced plant populations, genotypes with low production of secondary compounds may be selected for because of a release from natural enemies in the invasive range (Blossey and Nötzold 1995). This should be further investigated by measuring secondary compounds in native and invasive genotypes, especially alkaloids, that are known to be produced in large quantities by reed canarygrass (Lavergne and Molofsky 2004, and references therein).

These data suggest that *P. arundinacea* has the potential to adapt to a wide range of light and CO₂ conditions during the short term, and has high genetic variance (potential response to selection) for high CO₂ efficiency. While the instantaneous CO₂ response curves we observed are not indicative of the potential of this species to acclimate to long term increases in CO₂, the instantaneous and short term responses we observed show that certain genotypes of *P. arundinacea* may take advantage of fluctuating atmospheric CO₂, especially increasing its efficiency for CO₂ utilization. This trait could be particularly beneficial for populations in the invasive range growing along roadsides and waste-places where anthropogenic CO₂ inputs are highly variable. The tradeoff between enhanced photosynthetic rates and morphological plasticity should be investigated.

Overall, of the genotypes observed in this study, it is evident that the FR genotypes were physiologically and morphologically different from the CZ, VT and NC genotypes. While it is evident from this study and others that *P. arundinacea* has the evolutionary potential for hybridization events to produce morphologically superior genotypes, the evolution of physiological characteristics appears to be more conservative for this species. It is evident, however, that high variability exists amongst genotypes of *P. arundinacea* for responses to both changing light and CO₂ conditions, but how much that variability contributes to fecundity in comparison to morphological plasticity has yet to be determined. Impending climatic changes will ultimately determine which morphological and physiological traits will be most heavily selected for, but it is evident from this study that morphological plasticity may have more potential to determine a species' success in its native or

invasive ranges due to the conservative genetic nature of physiological traits.

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