Trait Convergence and Plasticity Among Native and Invasive Species in Resource-Poor Environments

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Functional traits provide a valuable conceptual basis for describing variation in plant ecological strategies, the distribution and abundance of species, and mechanisms of coexistence and community assembly as well as for predicting ecological effects and responses of plant communities to their environment (Weber and Keddy, 1999; Diaz and Cabido, 2001; Lavoie and Garnier, 2002; Suding et al., 2008). Alternative hypotheses about mechanisms of invasion and invasion resistance differ in their prediction of how functional traits and trait plasticity are expected to contribute to native and invasive species. For example, hypotheses based on habitat filtering and neutral processes predict that invasive species and dominant native species should have similar trait values and low trait plasticity. Invasive species may increase the tradeoff between growth and reproduction because they have to compete under higher environmental conditions for resources (Thompson et al., 1995; Duncan and Williams, 2002; Daloze et al., 2009). Alternatively, hypotheses based on similarity between native and invasive species as well as hypotheses based on leaf and root tissue economics predict that invasive species have more efficient trait values and lower specific leaf area (SLA) than native species. For example, herbivory, mechanical and fire disturbance may have increased the trait values and decreased the specific leaf area of invasive species compared to native species. These mechanistic hypotheses, in turn, provide the ecological basis for predicting and managing plant invasions (James et al., 2010) as well as for improving our understanding of invasion impact on ecosystems.

Given the importance in understanding functional trait variation, a substantial amount of research has focused on describing differences in trait values and trait plasticity between native and invasive species. Recent quantitative syntheses of this literature have demonstrated several strong and important patterns of functional trait variation between native and invasive species. Given the importance in understanding functional trait variation, these results do not mean that native and invasive leaf traits as well as meta-analysis have demonstrated that invasive species tend to produce thinner and less dense leaves than native species, resulting in a higher specific leaf area (SLA) (Leishman et al., 2007; van Kleunen et al., 2010). With respect to carbon assimilation and allocation, a higher SLA allows invasive species to achieve a greater return on biomass invested in leaves and allows invasive species to achieve greater root and shoot growth rates than native species (Lambers and Poorter, 1995). Thus, understanding functional trait convergence or divergence among invasive and native species as well as environmental constraints on trait plasticity is a key step toward refining general hypotheses of invasiveness and identifying effective targets of invasion management.


regime, soil moisture, and competitive interactions (e.g., with neighboring plants). The bulk of this work has focused on the interactions of water and nutrient stress on key functional traits such as leaf size, leaf economics spectrum (LES), and growth form. The LES describes the trade-off between the acquisition of carbon and nitrogen and the maintenance of transpiration efficiency. The growth form describes the shape and size of the plants, which can influence their ability to access resources and compete with other species. The key functional traits that are important in determining the success of native and invasive species are leaf area, biomass, and growth form.

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Aims: To understand the interactions of water and nutrient stress influencing key growth, resource capture, and resource conservation traits, as well as to evaluate the importance of traits related to nutrient availability during growth and allocation responses.

Methods: The experiment was conducted in a glasshouse using two species of native and invasive plants. Independent variables included water and nutrient treatments (high and low nutrient, high and low water). The response variables included growth, resource allocation, and resource conservation traits. Statistical analyses were performed using R software, and the relationships between traits were examined using principal component analysis.

Results: The results showed that both water and nutrient availability significantly influenced growth, allocation, and conservation traits. In general, the invasive species exhibited greater plasticity in response to changes in water and nutrient availability compared to the native species. This plasticity was associated with increased resource capture and conservation efficiency, allowing the invasive species to grow faster and allocate resources more efficiently under varying conditions.

Conclusion: The results highlight the importance of considering both water and nutrient availability in understanding the growth and allocation strategies of native and invasive species. The invasive species' greater plasticity suggests a potential competitive advantage in highly variable environments. Further research is needed to understand the underlying mechanisms driving these plasticity differences and how they relate to broader ecosystem processes.
For all four contrasts, significant differences existed among native and invasive species (Table 1). At high N and water availability, native species tended to have lower values for most growth-related traits than did invasive species (i.e., total biomass, RMRR, and SLA). At high N, low water availability, the trend was reversed, with native species having equivalent or slightly higher values for total biomass, RMRR, and RGR; only SLA tended to be higher for the invasive species at high N, low water availability. Similarly, patterns were observed at low N, high water, with invasive species having values nearly equivalent to native species at high N, high water availability, with invasive species tending to have higher values than native species for most growth-related traits (i.e., biomass, RMRR, and SLA). At low N, low water availability, invasive species tended to have higher biomass and higher SLA, but native species tended to have slightly higher RGR and RMRR.

Water potential, photosynthetic rate, and water-use efficiency—Nitrogen availability, water availability, functional group, and the interaction of N and water all significantly affected water potential, photosynthetic rate, and water-use efficiency (Table 2A, Fig. 2). All other effects were not significant. For all predictor variables, water potential and WUE were inversely correlated with photosynthetic rate (Table 2B); as water potential became increasingly negative and plants became more water-use efficient, photosynthetic rate declined (Fig. 2A–C). The responses to N and the interaction of N and water were most strongly driven by WUE, with slightly higher WUE at higher N availability; additionally, WUE tended to be greater under the combination of high N and low water than low N and low water availability (Fig. 2B). In contrast, the responses to water availability and functional group were most strongly driven by water potential (Table 2B). Plants grown at low water availability tended to have lower water potentials than plants grown at high water availability, and perennial grasses tended to operate at lower water potentials than the forbs (Fig. 2C).

In general, native and invasive species responded similarly to changes in resource availability with respect to water potential, photosynthetic rate, and WUE (Table 2C). Only the contrast comparing native and invasive species at low N, high water was marginally significant. Native species tended to operate at lower water potentials and higher WUE than invasive species in this treatment combination, but invasive species tended to maintain higher photosynthetic rates.

Nitrogen allocation and conservation—Traits related to N allocation and conservation were significantly affected by N, water, functional group, N × W, and N × functional group; all other factors were not significant (Table 3A, Fig. 3). Differences in N described the greatest proportion of the variation in traits due to N, functional group, N × W, and N × functional group (Table 3B). There was a trend for lower low N plants to have lower N and water availability, with N 1.5- to 2.5-fold higher under high N, high water availability compared with all other treatments in most species (Fig. 3A). Differences in NUE described the greatest proportion of the variation in traits due to water availability (Table 3B), with PWNUE 1.9-fold under low water availability (Fig. 3B). Overall, green and senesced leaf N tended to be higher under lower N and water availability (Fig. 3C–D).

Few differences were observed between native and invasive species for N allocation and conservation traits (Table 3C). The only significant contrast was comparing native and invasive species at high N, low water availability. Native species tended to have higher green leaf N and NPUE than invasive species, but lower PNUE and senesced leaf N in invasive species under this treatment (Fig. 3A–D).

Nitrogen pool data indicate that both N and water availability influenced N pool size in most species (Fig. 4). In general, plants grown at high N tended to have greater total N pools than plants grown at lower N. However, water availability limited total N pool size. Roots and green leaves accounted for the majority of the total N pool across treatments. However, as resource availability decreased, root N pool accounted for a greater proportion of the total N pool. These changes in root N pool could be linked to increased root biomass allocation under resource-poor conditions.

Relationships among functional traits, species, and resource availability—Overall, the average RGRs and WUEs were arranged along the first axis of the PCA to soil water availability: this axis explained 90.0% of the variation in the data. Samples associated with the right side of the first axis and samples associated with low water availability were located on the right side of the first axis (Fig. 5). Thus, plants grown at high water availability were associated with higher PNUE, NP, and total biomass. In contrast, plants grown at low water availability were associated with higher N, more negative water potentials, greater WUE, and greater RGR. The second axis explained 12.6% of the variation in the data and was most strongly associated with RMR. This axis was associated with neither N nor water availability. Although some diffuse grouping could be observed for some species (e.g., S. monrovia and P. spinata), neither axis was associated with either morphology or origin, with strong overlap in trait responses between native and invasive species, as well as among perennial grasses and perennial forbs.

Plasticity in functional traits—As assessed by RDPs, plasticity did not differ between native and invasive species for the suite of growth and allocation traits measured (F₁₆, 80 = 0.60, P = 0.66). Of the four traits, total biomass was the most plastic, with RDPs ranging from 0.34-0.39 (Table 4). Relative growth rate varied little across N and water availability, and RMR and SLA were fairly constant across treatments, with mean RDI values as low as 0.005 calculated for SLA (Table 4A). Overall, SLA was the least plastic in response to variation in resource availability of the 11 traits evaluated.

In contrast, plasticity values for water potential, photosynthetic rate, and WUE were significantly different between native and invasive species (F₁₆, 80 = 5.12, P = 0.000). Across all three traits, invasive species were significantly more plastic than native species. Of all the functional traits measured, photosynthetic rate was the most plastic in response to variation in resource availability (Table 4B).

Additionally, a marginally significant difference in plasticity was found between native and invasive species for traits related to N allocation and conservation (F₁₆, 80 = 2.73, P = 0.048). Although plasticity values for senesced leaf N and PNUE were similar between native and invasive species, plasticity in green leaf N and PNUE was greater for invasive compared with native species (Table 4C).
For all four contrasts, significant differences existed among native and invasive species (Table 1C). At high N and water availability, native species tended to have lower values for most growth-related traits than did invasive species (i.e., total biomass, RMR, and SLA). At high N, low water availability, the trend was reversed, with native species having equivalent or slightly higher values for total biomass, RMR, and RGR; only SLA tended to be higher for the invasive species at high N, low water availability. Similar patterns were observed at low N, high water availability, with invasive species tending to have higher values than native species for most growth-related traits (i.e., biomass, RMR, and SLA). At low N, low water availability, invasive species tended to have higher biomass and higher SLA, but native species tended to have slightly higher RGR and RMR.

Water potential, photosynthetic rate, and water-use efficiency—Water potential, photosynthetic rate, and water-use efficiency were consistent among functional groups and the interaction of N and W significantly affected water potential, photosynthetic rate, and water-use efficiency (Table 2A, Fig. 2). All other effects were not significant. For all predictor variables, water potential and WUE were inversely correlated with photosynthetic rate (Table 2B); as water potential became increasingly negative and plants became more water-use efficient, photosynthetic rate declined (Fig. 2A-C). The responses to N and the interaction of N and W were most strongly driven by WUE, with slightly higher WUE at higher N availability, and WUE tended to be greater under the combination of high N and low water than low N and low water availability (Fig. 2B). In contrast, the responses to water availability and functional group were most strongly driven by water potential (Table 2B). Plants grown at low water availability tended to have lower water potentials than plants grown at high water availability, and perennial grasses tended to operate at lower water potentials than the forbs (Fig. 2C).

In general, native and invasive species responded similarly to changes in water availability with respect to water potential, photosynthetic rate, and WUE (Table 2C). Only the contrast comparing native and invasive species at low N, high water was marginally significant. Native species tended to operate at lower water potentials and higher WUE than invasive species in this treatment combination, but invasive species tended to maintain higher photosynthetic rates.

Nitrogen allocation and conservation—Traits related to N allocation and conservation were significantly affected by N, water, functional group, N x W, and N x functional group; all other factors were not significant (Table 3A, Fig. 3). Differences in NP described the greatest proportion of the variation in traits due to N, functional group, N x W, and N x functional group (Table 3B). There was a trend for lower NP with reduced N and water availability, with NP 1.5–2.5-fold higher under high N, high water availability compared with all other treatments in most species (Fig. 3A). Differences in PNUDE described the greatest proportion of the variation in traits due to water availability (Table 3B), with 1.9-fold higher under low water availability (Fig. 3B). Overall, high and green senesced leaf N tended to be higher under lower and water availability (Fig. 3C–D).

Few differences were observed between native and invasive species for N allocation and conservation traits (Table 3C). The only significant contrast was comparing native and invasive species at high N, low water availability. Native species tended to have higher green leaf N and NP than invasive species but lower PNUDE and senesced leaf N in invasive species under this treatment (Fig. 3A–D).

Nitrogen pool data indicate that both N and water availability influenced N pool size in most species (Fig. 4). In general, plants grown at high N tended to have greater total N pools than plants grown at lower N. However, water availability limited total N pool size, even under high N conditions. Thus, although green leaf N tended to increase at lower water availability, the decrease in biomass lowered water availability limited total N pool size. Root and green leaves accounted for the majority of the total N pool across treatments. However, as resource availability decreased, root N pool accounted for a greater proportion of the total N pool. These changes in root N pool can be linked to increased root biomass allocation under resource-poor conditions.

Relationships among functional traits, species, and resource availability—Overall, the average N and W responses were arranged along the first axis with respect to soil water availability; this analysis explained 80% of the variation in the data. Samples associated with the first axis were located on the left side of the first axis, and samples associated with lower water availability were located on the right side of the first axis (Fig. 5). Thus, plants grown at high water availability were associated with higher PNUDE, NP, and total biomass. In contrast, plants grown at low water availability were associated with higher senesced leaf N, more negative water potentials, greater WUE, and greater RMR. The second axis explained 12.6% of the variation in the data and was most strongly associated with RMR. This axis was associated with neither N nor water availability. Although some diffuse grouping could be observed for some species (e.g., S. minima and P. spinosa), neither axis was associated with other morphology or origin, with strong overlap in trait responses between native and invasive species, as well as among perennial grasses and perennial forbs.

Plasticity in functional traits—As assessed by RDPs, plasticity did not differ between native and invasive species for the suite of growth and allocation traits measured (F[1, 60] = 0.65, P = 0.002). Across all three traits, invasive species were significantly more plastic than native species. Of all the functional traits measured, photosynthetic rate was the most plastic in response to variation in resource availability (Table 4B). Additionally, a marginally significant difference in plasticity was found between native and invasive species for traits related to N allocation and conservation (F[1, 6] = 2.73, P = 0.048). Although plasticity values for senesced leaf N and PNUDE were similar between native and invasive species, plasticity in green leaf N and NP was greater for invasive compared with native species (Table 4C).

In contrast, plasticity values for water potential, photosynthetic rate, and WUE were significantly different between native and invasive species (F[1, 6] = 5.12, P = 0.000). Across all three traits, invasive species were significantly more plastic than native species. Of all the functional traits measured, photosynthetic rate was the most plastic in response to variation in resource availability (Table 4B).

Discussion

In support of our first hypothesis, invasive species achieved greater biomass than native species under both low and high N, when water supply was high. For example, at high N, high water availability, invasive species had higher biomass than...
native species, though RGR was similar between the species groups. At high N, low water availability, natives maintained similar total biomass but a slightly higher RGR than invasive species. Thus, although biomass and RGR declined in response to decreased water availability, both native and invasive species, the species group achieving higher biomass and/or RGR under a given treatment combination depended on soil water availability. In contrast, invasive species had higher total biomass but slightly lower RGR than native species under both the low N treatments, regardless of water availability. Under all treatment combinations, invasive species had higher SLA than native species. Constructing cheaper tissues may provide invasive species a growth advantage under both low N and high N (Lammers and Pootar, 1992) as well as under well-watered conditions (Gredlop and Rejmanek, 2007; James and Denovsky, 2007; James, 2008). However, under low water availability, high SLA may be disadvantageous, as it provides greater surface area for transpiration (Lammers et al., 2008). Additionally, maintaining a higher RMR than natives under both high N, high water and low N, high water may have provided invasives with greater access to soil nutrients (Aerts and Chapin, 2000). At lower water availability, N allocation to leaves was higher than that to roots, indicating higher RGR. Invasive species tended to allocate more photosynthesis to roots and MUE, WUE, and NUE at lower water availability, driven in large part by strong declines in stomatal conductance (data not shown). High water potentials indicate plant water status during the most stressful portion of the day, when plants are balancing radiation heat loads with transpiration. In the high water treatment, drought also had strong physical processes that influence soil water availability. In this study, drought limits nutrient supply to roots by decreasing N movement through soils via diffusion or mass flow (Dunham and DeNardo, 2008). Drought limits nutrient availability to roots by reducing nutrient mobility in the soil, and reduced transpiration rates limit nutrient mass flow rates through soil, both of which limit nutrient availability for plant uptake.

Many authors have argued that high N availability favors invasive species, because high N promotes nutrient mobility in the soil, and reduced transpiration rates limit nutrient mass flow rates through soil, both of which limit nutrient availability for plant uptake.
native species, though RGR was similar between the species groups. At high N, low water availability, natives maintained similar total biomass but a slightly higher RGR than invasive species. Thus, although biomass and RGR declined in response to decreased water availability, both native and invasive species, the species group achieving higher biomass and/or RGR under a given treatment combination depended on soil water availability. In contrast, invasive species had higher root biomass but slightly lower RGR than native species under both the low N treatments, regardless of water availability. Under all treatment combinations, invasive species had higher SLA than SLA than natives. Constructing cheaper tissues may provide invasive species a growth advantage under both low N and high N (Lambers and Poorter, 1992) as well as under well-watered conditions (Goudkopp and Rejmanek, 2007; James and Drenovsky, 2007; James, 2008). However, under low water availability, high SLA may be disadvantageous, as it provides greater surface area for transpiration (Lambers et al., 2008). Additionally, maintaining a higher RMR than natives under both high N, high water and low N, high water may have provided invasives with greater access to soil nutrients (Aerts and Chapin, 2000). At lower water availability, native species had higher total biomass than did invasive species. Increased allocation to roots under drought conditions is a key adaptation to maintaining plant water status.

![Graph showing gas exchange and water potential traits of native and invasive perennial species.](image-url)

**Fig. 2.** Gas exchange and water potential traits of native and invasive perennial species, including (A) photosynthetic rate, (B) instantaneous water-use efficiency (WUE), and (C) plant water potential. Data are means ± SE (N = 3–5). See Note 1 for legend of abbreviations. (Lambers et al., 2008), enabling native species to maintain greater biomass than invasive species under decreased water availability. In contrast to the initial hypotheses, native and invasive species were similar with respect to instantaneous physiological measurements, including midday water potential, photosynthetic
泌，总养分，低水

4. Total nitrogen (N) pools of native and invasive potential spe-
   cies. (A) N productivity (PNUE), (B) photosynthetic N use efficiency
   (PNUE), (C) green leaf N, and (D) senesced leaf N. Data are means ± SE (N = 6). Note: See Fig. 1 legend for definitions of abbreviations.

Multiple resource limitations constrain plant growth and
   plasticity and may be particularly strong drivers of plant growth
   and function in arid, nutrient-poor systems (Blom, 1985; Gleen
   son and Tilman, 1992; James et al., 2005; Valladares et al.,
   2007). The influence of multiple resource limitations on patterns
   of trait convergence or divergence as well as trait plasticity
   among native and invasive species has direct implications for
   advancing theories of invasion and invasion resistance. In this
   study, invaders tended to have higher SLA, supporting the no-
   tion that invasive species tend to be positioned further along the
   leaf economics spectrum toward resource capture (Wright et al.,
   2004). We also found, however, strong evidence for functional
   similarity and plasticity between native and invasive species,

particularly with respect to nutrient allocation and conserva-
   tion traits, supporting community assembly hypotheses based
   on habitat filtering (Tecco et al., 2010). Importantly, our data show
   that multiple resource limitations influence the degree of trait
   convergence or divergence between invasive and native spe-
   cies. The limited number of species used in this study and the
   lack of phylogenetically controlled comparisons constrain our
   ability to generalize beyond our particular system. Neverthe-
   less, these data make a strong case for improved understanding
   of how multiple resource and environmental stressors influence
   differences in resource conservation and resource capture traits
   between native and invasive species if we are to further ad-
   vance theories of invasion and invasion resistance.

LITERATURE CITED

Arizzi, R. 1996. Nutrient resorption from senescing leaves of perennial

Arizzi, R. 1999. Interspecific competition in natural plant communi-
   ties: mechanisms, trade-offs and plant-soil feedbacks. Journal of

Arizzi, R., and P. S. Couvreur. 2000. The mineral nutrition of wild
   plants revisited: A re-evaluation of processes and patterns. Advances in

   Baker and G. L. Sebbens (eds.). Genetics of coexisting species, 147–

Berendse, F. 1994. Competition between plant populations at low and

   tion in plants—An economic analogy. Annual Review of Ecology and
   Systematics 16:363–392.

Fig. 3. Nitrogen (N) allocation and conservation traits of native and invasive potential species, including (A) N productivity (PNUE), (B) photosynthetic
   N use efficiency (PNUE), (C) green leaf N, and (D) senesced leaf N. Data are means ± SE (N = 6). Note: See Fig. 1 legend for definitions of abbreviations.
and conservation patterns. Plants with higher PNUE and lower senesced leaf N (and thus greater resource efficiency, seeou Killingbeck, 1996) had enhanced plant performance, as assessed by total plant biomass, at the end of the experiment (P < 0.005 for both variables; data not shown). These correlations stress the importance of resource conservation traits for the success of invasive species in resource-poor systems, and further research and emphasis should be placed on these traits in invasive species. Without data on traits such as nutrient-use efficiency, mean net photosynthesis, resorption, and storage, we will fail to recognize key mechanisms supporting the role of invasive species in resource-poor environments.

Contrary to expectations, native and invasive species were similarly plastic for most measured traits. The greatest differences in plasticity between native and invasive species were observed for instantaneous measurements (A, WUE, and plant water potential), with invasive species being more plastic in response to resource availability for all three traits. Although there was a marginally significant difference in plasticity for N allocation and conservation traits, no difference in plasticity existed between native and invasive species, for growth and allocation traits. These results are similar to those of a study comparing related species of invasive and native woody vines, in which native and invasive species had similar plasticity for 14 out of 17 physiological and growth traits measured, though overall plasticity was greater in invasive than in native species (Ouonskaya et al., 2010).

Likewise, in two phylogenetically paired studies of native and invasive species across a range of life forms, native and invasive species did not differ in their plasticity for a suite of growths and physiological traits (Funk, 2008; Godoy et al., 2011). These studies suggest plasticity alone may not predict the success of invasive species. Finally, plasticity varied greatly depending on the trait measured and was not consistent among the trait groupings. The most plastic traits generally were those that require only small changes in allocation of resources or functioning and/or are fairly reversible, such as photosynthetic rate, PNUE, total biomass, and N. In contrast, those traits that require (or are strongly influenced by) more long-term changes in tissue construction were less plastic, such as RGR, SLA, green leaf N, and senesced leaf N, which were the least plastic traits.

Multiple resource limitation constrain plant growth and plasticity and may be particularly strong drivers of plant growth and function in arid, nutrient-poor systems (Bloom et al., 1985; Gleeson and Tilman, 1992; James et al., 2005; Valladares et al., 2007). The influence of multiple resource limitations on patterns of trait convergence or divergence as well as trait plasticity among native and invasive species has direct implications for advancing theories of invasion and invasion resistance. In this study, invasives tended to have higher SLA, supporting the notion that invasive species tend to be positioned further along the leaf economics spectrum toward resource capture (Wright et al., 2004). We also found, however, strong evidence for functional similarity and plasticity between native and invasive species.


