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Superior performance and nutrient-use efficiency of invasive plants over non-invasive congeners in a resource-limited environment

Virginia Matzek

Abstract Invasive plant species are often found to have advantages over native species in growth-related traits, such as photosynthetic rate, in disturbed or resource-rich environments. However, resource-use efficiency, rather than opportunistic resource capture, may confer more advantages when resources are scarce. In this study, performance and functional traits of invasive and non-invasive members of the genus *Pinus* were contrasted under the condition of nutrient limitations. Invasive species outperformed non-invasive congeners by growing 28% faster, on average. Invasives and non-invasives did not differ in biomass allocation traits (root-weight ratio, stem-weight ratio, leaf-weight ratio, leaf area ratio, root: shoot coefficient), but invaders had thinner and/or less dense leaves, as shown by a significantly lower leaf mass per area and leaf dry mass fraction. No differences between invasives and non-invasives were apparent in area-based leaf content of nitrogen, chlorophyll, or total protein, nor did the two groups differ in how efficiently they took up nutrients (specific absorption rate per unit root mass). The trait most strongly associated with invasives' superior performance was photosynthetic nitrogen-use efficiency. Non-invaders were more water-use efficient. The results suggests that the relative performance of invasive and non-invasive species is context-dependent. Invaders may allocate leaf nitrogen more efficiently to maximize photosynthesis and growth in nitrogen-poor soils, while non-invaders with more heavily defended leaves may have an advantage in drier areas. Rather than searching for a suite of traits that constitutes "invasiveness", it may be necessary to identify potential invaders by traits that are most adaptive to the local resource context.

Keywords Biomass allocation · Invasiveness · Nutrient limitation · Nutrient-use efficiency · Plant traits · Water-use efficiency

V. Matzek (✉)
Department of Environmental Studies, California State University-Sacramento, 6000 J Street, Sacramento, CA 95819, USA
e-mail: vmatzek@csus.edu

Introduction

There is as yet no single or unified explanation for why some plant species become invasive outside their native ranges and others do not. Some researchers have looked for answers in competitive or facilitative interactions between the invader and organisms of its host range, including allelopathy, zoochory and release from natural enemies [for reviews, see Shea and Chesson (2002), Hierro et al. (2005)]. Others have identified intrinsic plant traits such as seed size, plant height, or growth rate, that distinguish invaders

from non-invaders [for a review, see Pyšek and Richardson (2007)].

The focus on plant traits is partly driven by the hope that identifying a suite of traits associated with invasiveness will help predict which species are potential invaders before their introduction. Traits commonly linked to invasiveness include several that indicate a resource-exploitative strategy, such as high relative growth rate (Forcella et al. 1986; Burns 2004; Wilson et al. 2004; Garcia-Serrano et al. 2005; Burns 2006; Leicht-Young et al. 2007; Gurevitch et al. 2008), low leaf mass per unit area (Pammenter et al. 1986; Durand and Goldstein 2001a; Grotkopp and Rejmánek 2007; Deng et al. 2004; Feng and Fu 2008), and high photosynthetic rate (Baruch and Goldstein 1999; Durand and Goldstein 2001b; McDowell 2002; Funk and Vitousek 2007). This set of traits dovetails nicely with the observation that invaders commonly invade high-resource disturbed areas (Burke and Grime 1996; Daehler 2003) or else invade by virtue of novel traits that increase local resource ability, such as N-fixation or flammability (Vitousek and Walker 1989; Brooks et al. 2004).

Several attempts at a theory to explain invasion success have focused on the importance of resource availability, most notably the fluctuating resources hypothesis (Davis et al. 2000), in which the invader or its propagules are latent in the environment until a chance disturbance event increases resource availability to the point where the more exploitative invader can gain a foothold. Following on Alpert and colleagues' contention (2000) that the relative performance of invaders varies with environmental stress, a review by Daehler (2003) provided convincing evidence that invaders' success was "context-dependent"—namely, that instances of invaders consistently outperforming native species were rare, and that natives often outperformed invasives when resource availability was low. These observations have given rise to experiments designed to decrease resource availability, particularly soil nutrient availability, as a management strategy to defeat invaders (Blumenthal et al. 2003; Corbin and D'Antonio 2004; Török et al. 2000; Blumenthal 2009; Funk and McDaniel 2010).

However, because these experiments have met with mixed success, and because we also observe invaders to outperform natives even in extremely harsh environments (Pavlik 1983; Pammenter et al. 1986), it is worth asking whether invasive species

cannot, in fact, beat native species at their own (efficient) game. A review of the literature on alien-native comparisons by Pyšek and Richardson (2007) showed that a finding that aliens/invasives were more water- or nutrient-use efficient than native species was somewhat more frequent than finding that invaders grew faster or had lower LMA. Very few studies have compared invaders and non-invaders in low-resource environments, and even fewer of those have controlled for phylogenetic effects by comparing closely related species. In a notable exception, Funk and Vitousek (2007) found that invaders had generally greater instantaneous resource-use efficiency in water-, light-, or nutrient-limited environments than their non-invasive counterparts, and suffered no detriment compared to native species when differences in leaf lifespan were accounted for.

For this study, I compared the performance under nutrient-poor conditions of five invasive and five non-invasive species in the genus *Pinus*, and measured physiological and morphological traits related to resource use and capture in each group. Pines are a good study system for such comparisons because they have been widely planted around the world, and it is thus possible to compare known invaders to species that have been introduced outside their range but have not been found to be invasive. This approach has advantages over comparing invasives to "native" species whose invasiveness is actually unknown because they have not been introduced elsewhere (Rejmánek 2000; Muth and Pigliucci 2006). Working within a single genus also helps control for phylogenetic differences among native and invasive species.

I hypothesized that, under conditions where plants were limited by both N and P, invasives would only outperform non-invasives in growth rate if they were able to capture or use nutrients more efficiently. Specifically, I hypothesized that rates of nutrient uptake by roots, and photosynthetic nutrient-use efficiency by leaves, would be higher in the faster-growing group of species.

Methods

Experimental design

Five invasive pines (*Pinus banksiana, P. halepensis, P. muricata, P. pinaster* and *P. radiata*) and five non-

invasive pines (*P. cembra, P. flexilis, P. lambertiana, P. sabiniana* and *P. torreyana*) were included in the study. Information on invasiveness comes from the work of Grotkopp et al. (2002), Rejmánek and Richardson (1996). "Invasive" means having a known record of invasiveness on at least two continents, while "non-invasive" means being planted on at least three continents with no reports of invasive behavior (Grotkopp et al. 2002). Invasive species chosen also had highly positive Z scores, and non-invasive species negative Z scores, where the Z score is a discriminant function combining the traits of mean seed mass, minimum juvenile period, and mean interval between large seed crops, traits that maximized the difference between invaders and non-invaders in a previous study (Rejmánek and Richardson 1996). [The traits measured in this paper (Table 1) were not among those considered by Rejmánek and Richardson (1996) in creating the discriminant function].

Seeds obtained from commercial nurseries were cold stratified according to species requirements (Young and Young 1992), germinated in a sand-vermiculite mixture, and transplanted into 35L pots in a greenhouse when their second set of true leaves emerged, to minimize ontogenetic differences between species. Nine seedlings of each species

(except *P. cembra*; $n = 7$) were grown with nitrogen supply of 1 mg N pot^{-1} wk^{-1} and phosphorus supply of 0.2 mg P pot^{-1} wk^{-1}. In a separate set of growth experiments using increased amounts of N and P (Matzek, unpublished data), this low level of nutrient supply was shown to be significantly growth-limiting to all species, resulting in an average reduction of RGR by 50%. Other nutrients were supplied in abundance as a half-strength N- and P-free Hoagland's solution, and soil moisture was monitored with a probe to ensure that water was not limiting to plant growth. Average midday PAR at plant height was approximately 1,350 μmol/m^2/s. Daytime temperatures were $\sim 25°C$ and nighttime temperatures $\sim 15°C$ and greenhouse daylength was set at 12 h.

Relative growth rate and morphological traits

Twenty additional seedlings of each species (except *P. cembra*; $n = 13$) were selected randomly for destructive harvest at transplant size to estimate the "initial" size of seedlings for RGR calculations. RGR calculations were performed according to the equations of Causton and Venus (1981) and are expressed as the total plant dry biomass per unit of initial (seedling) dry weight per unit time. Specific absorption rate (SAR) was calculated similarly, from initial

Table 1 Definitions and abbreviations of traits measured

Trait	Description	Units
RGR	Relative growth rate	g plant g^{-1} init wt d^{-1}
LMR	Leaf mass ratio	g leaf g^{-1} plant
RMR	Root mass ratio	g root g^{-1} plant
SMR	Stem mass ratio	g stem g^{-1} plant
DMF	Dry mass/fresh mass ratio	
LMA	Leaf mass per unit area	mg leaf cm^{-2}
k	*Root* shoot allometric coefficient	
SAR$_{nitrogen}$	Specific absorption rate of N	mg N gain g^{-1} root d^{-1}
SAR$_{phosphorus}$	Specific absorption rate of P	mg P gain g^{-1} root d^{-1}
Protein$_{area}$	Protein content per unit area	mg protein cm^{-2} leaf
P$_{area}$	Phosphorus content per unit area	g P m^{-2} leaf
N$_{area}$	Nitrogen content per unit area	g N m^{-2} leaf
Chl$_{area}$	Chlorophyll ($a + b$) content per unit area	μg chl cm^{-2} leaf
Chl a/b	Chlorophyll *a–b* ratio	
A$_{mass}$	Photosynthetic rate per unit mass	nmol CO$_2$ g^{-1} leaf s^{-1}
A$_{area}$	Photosynthetic rate per unit area	μmol CO$_2$ m^{-2} leaf s^{-1}
PNUE	Photosynthetic nitrogen-use efficiency	μmol CO$_2$ g N^{-1} s^{-1}
WUE	Water-use efficiency	μmol CO$_2$ mmol^{-1} H$_2$O s^{-1}

and final biomass measurements and nutrient concentrations, as the net gain of nutrient per unit root mass per day, integrated over the harvest interval of 84 days.

To assess ongoing plant partitioning of carbon between roots and shoots, independent of ontogenetic drift, I calculated the root–shoot allometric coefficient, k. If the dry weights of roots and shoots of a plant are related by the function:

$$M_{root} = bM_{shoot}^{K}$$

where b is a constant and k the allometric coefficient, then

$$\log M_{root} = \log b + k \log M_{shoot}$$

and k is estimated as the slope of the reduced major axis regression on the pairs of ln-transformed root and shoot weights at initial and harvest age time points.

Biomass allocation traits (leaf mass ratio *LMR*, shoot mass ratio *SMR* and root mass ratio *RMR*) were calculated as the proportion of whole-plant dry mass found in leaves, shoots, or roots, respectively.

Photosynthesis and physiological traits

Plants were harvested after 12 weeks growth in the low nutrient treatment. Photosynthetic rate was measured immediately prior to harvest by gas exchange, on a detached shoot tip enclosed in the conifer chamber of a portable infrared gas analyzer (LI-6400, LiCor, Lincoln, Nebraska, USA). Measurements were made under conditions expected to produce maximal rates of photosynthesis, i.e., outdoors in full sun, generally between 9 a.m. and noon, when temperatures were moderate (20–30°C) and relative humidities in the range of 70–75%. CO_2 input was fixed at 400 ppm and airflow through the chamber was 500 μmol/s. Measurements were made as soon as the CO_2 concentration in the chamber stabilized, typically <2 min. Self-shading was minimized by orienting the chamber so that the shoot tip was maximally illuminated. The maximal photosynthetic rate was calculated on mass (A_{mass}) and area (A_{area}) bases while photosynthetic nitrogen-use efficiency was calculated as the ratio of A_{area} and N_{area} or P_{area} (μmol CO_2 g N^{-1} s^{-1}), using the photosynthetic rate of individuals in each species and the value for N

or P concentration from the species tissue composite (below). Water-use efficiency (WUE) was calculated as the ratio of photosynthesis to transpiration (μmol CO_2 mmol H_2O^{-1} s^{-1}).

At harvest, the two youngest whorls of needles at each shoot tip (one fully expanded, one mid-expansion) were removed, weighed and flash frozen in liquid nitrogen. The frozen leaf tissue was composited by species, ground in liquid nitrogen with a mortar and pestle, and either stored at −80° C for use in protein and chlorophyll measurements, or oven-dried at 55°C for assays of N and P concentration by Kjeldahl digest. The remaining root, stem and leaf tissue were separately weighed and oven-dried at 55°C, and dry mass fraction (DMF) was calculated as the ratio of fresh mass to oven-dried mass. Fresh mature needles from 3 to 4 harvested individuals of each species were scanned on a flatbed scanner before being dried and weighed, and their projected leaf area was analyzed with the public domain software program NIH Image 1.63. Protein, chlorophyll and nutrient content results are expressed on an area basis, rather than a mass basis, to avoid confounding with the separately measured trait of leaf mass per unit area (LMA).

To assay protein content, frozen leaf tissue was heated to 55°C in a buffer consisting of 5% sucrose, 5% sodium dodecyl sulfate and 5% β-mercaptoethanol (Ekramoddoullah 1993). The resulting extract was subjected to the Lowry assay, using a commercial kit (Bio-Rad Laboratories, California, USA) compatible with detergents and reducing agents. Chlorophyll was extracted from frozen leaf tissue in 100% acetone and determination of chl a and b concentrations was performed according to the equations of Lichtenthaler and Wellburn (1983) for absorbance measured at 662 and 645 nm, respectively.

Statistical analyses considered species as replicates ($N = 10$) and Student's t test was used to determine significant differences between the invasive and non-invasive groups of pines, except when non-normality required the use of the Wilcoxon rank-sum test. Rather than using the sequential Bonferroni to reduce experiment-wide type I error to 0.05, at the cost of significant inflation of the type II error, I follow the advice of Moran (2003) and report all exact P values, along with the probability of obtaining the relevant number of significant results from a

large number of independent tests. For the 18 planned trait comparisons here, the probability of obtaining by chance seven results with P values below $\alpha = 0.05$ is calculated to be 0.0000141.

Results

Results are summarized for invasive and non-invasive groups in Table 2; for species means, see Appendix—Electronic supplementary material. Using growth rate as the absolute measure of performance, invasive species significantly outperformed non-invasive congeners, growing 28% faster.

Invasives and non-invasives did not differ significantly in any trait related to biomass allocation: leaf mass ratio, root mass ratio, stem mass ratio, or root:shoot coefficient. However, invasive leaves had significantly lower leaf mass per unit area (LMA) and lower dry mass/fresh mass ratio, indicating thinner and/or less dense leaf construction. With differences

Table 2 Mean trait values for invasive and non-invasive species

Trait	Invasive mean	Non invasive mean	P value
RGR	0.0239 ± 0.0017	0.0187 ± 0.0012	**0.0216***
LMR	0.3951 ± 0.0272	0.371 ± 0.027	0.26
RMR	0.4881 ± 0.0422	0.5095 ± 0.0227	0.6667
SMR	0.1168 ± 0.0177	0.1195 ± 0.0163	0.9146
DMF	0.249 ± 0.012	0.304 ± 0.017	**0.0367***
LMA	0.0209 ± 0.001	0.0291 ± 0.0021	**0.0085**
k	1.87 ± 0.26	2.11 ± 0.12	0.4034*
$SAR_{nitrogen}$	1.08 ± 0.19	0.93 ± 0.11	0.5309*
$SAR_{phosphorus}$	0.31 ± 0.05	0.19 ± 0.04	0.0601*
$Protein_{area}$	0.368 ± 0.053	0.659 ± 0.182	0.1857
P_{area}	0.183 ± 0.023	0.387 ± 0.061	**0.0367***
N_{area}	1.341 ± 0.234	2.208 ± 0.361	0.0788
Chl_{area}	19.5 ± 2.3	33.0 ± 11.9	0.2981
Chl a/b	3.34 ± 0.09	3.47 ± 0.14	0.4584
A_{mass}	76.23 ± 13.58	40.77 ± 4.44	**0.038**
A_{area}	8.13 ± 1.75	5.85 ± 0.65	0.2546
PNUE	6.02 ± 0.45	2.99 ± 0.57	**0.0032**
WUE	1.52 ± 0.05	2.43 ± 0.38	**0.0216***

Abbreviations as in Table 1

Boldfaced values indicate significance

* Denotes non-parametric Wilcoxon rank-sum used rather than Student's t test

Table 3 Correlations between performance and traits differing among invaders and non-invaders

Trait	Correlation with RGR	P value
WUE	-0.685	**0.014**
DMF	-0.4439	0.099
LMA	-0.4711	0.058
P_{area}	-0.6664	**0.017**
A_{mass}	0.3947	0.13
PNUE	0.7262	**0.00867**

Boldface denotes statistically significant correlation coefficients

Correlation is between species' mean values for each trait ($N = 10$)

in LMA taken into account (i.e., by measuring leaf chemistry on an area basis), there were no significant differences in leaf content of nitrogen, protein, or chlorophyll between invasives and their non-invasive congeners, but non-invasives did have higher area-based phosphorus content than invaders. When leaf N, P, protein and chlorophyll were expressed on a mass basis, no significant leaf chemistry differences were apparent.

Traits related to resource capture were not exclusively the domain of either group of plants. No significant differences in specific absorption rate for either nitrogen or phosphorus were observed. Nor did chlorophyll a/b ratio, an indicator of allocation to light harvesting, differ among invasives and non-invasives. However, invasive species did have higher mass-based photosynthesis, and higher photosynthetic nitrogen-use efficiency (PNUE) while non-invaders were more water-use efficient (WUE).

Of the traits that were different between invasive and non-invasive groups, the three most closely related to performance (i.e., RGR) were WUE, PNUE and P_{area} (Table 3). Photosynthetic nutrient-use efficiency was strongly positively correlated with relative growth rate ($r = 0.7262$), while water-use efficiency was strongly negatively associated with RGR ($r = -0.6850$). Area-based P also was negatively associated with RGR ($r = -0.6664$).

Discussion

This study provides evidence that invasive species can outperform non-invaders under nutrient-limited

conditions, and that they can do so by being more nutrient-use efficient. It also links a morphological trait, the plant's LMA, to both the higher photosynthetic nitrogen-use efficiency of invasives and the higher water-use efficiency of non-invasives. Together, these lines of evidence suggest strongly that the relative performance of invasives in low-resource environments is context-dependent.

Performance

The performance indicator used here is the relative growth rate (RGR). A high relative growth rate is related to fitness and often makes for a successful competitive strategy, allowing plants to establish faster and outcompete their neighbors for resources. Because RGR is an exponential measure, small differences have profound implications for plant size in the early period of seedling establishment. Among phylogenetically controlled comparisons of invasive and native plants, high growth rate is often associated with the invasive species under higher-resource conditions (Forcella et al. 1986; Burns 2004; Wilson et al. 2004; Garcia-Serrano et al. 2005; Burns 2006; Gurevitch et al. 2008).

However, it is important to note that high RGR is not the only successful competitive strategy; in resource-poor environments, longevity and persistence may trump speed of growth. This short-term seedling experiment cannot address the comparative performance of invasives and non-invasives in terms of survivorship or reproductive fitness. Similarly, life-history traits associated with the ability to colonize new environments, such as seed size or fecundity, may be equally important to "invasiveness" but are not measured in this experiment.

Morphological traits

Invasive and non-invasive pines differed only modestly in morphology. At the whole-plant level, no measure of biomass allocation differed among the invasive and non-invasive groups. This result corresponds with an analysis of a larger group of pine species, in which leaf mass ratio was not significantly different between invasive and non-invasive species (Grotkopp et al. 2002). However, in a phylogenetically-controlled contrast of invasive and less-invasive woody angiosperms in California, more-invasive

species showed significantly greater allocation to roots, a potential advantage in the dry Mediterranean climate (Grotkopp and Rejmánek 2007). Of five phylogenetically matched pairs of invasive and native Hawaiian species occurring in low-resource habitats, four invaders had lower LWR, and three invaders had higher RMR, suggesting that invasive species frequently invested more biomass to foraging for soil resources in those environments (Funk 2008).

However, at the leaf level, invasive and non-invasive species were morphologically distinct, with invaders having significantly lower leaf mass per unit area (LMA) and dry-mass fraction (DMF). Since resource capture by plants in general is a phenomenon of fluxes across surfaces—gas exchange across the surface of the leaf, ion exchange across the surface of the root—leaves with higher surface area:mass ratio maximize gas exchange and photosynthetic capacity. Such leaves also risk greater damage from herbivory and breakage, and so their faster carbon gain may be offset by their shorter lifespan. The LMA seems to be the central trait in dictating where along the spectrum of carbon economy plants fall, from a slow-growth/high-persistence strategy to a fast-growth/low-persistence strategy (Wright et al. 2004). As observed here, invasive plants have often been found at the low-LMA end of this spectrum when compared to closely-related native or non-invasive species (Pammenter et al. 1986; Durand and Goldstein 2001a; Grotkopp et al. 2002; Deng et al. 2004; Wilson et al. 2004; Feng et al. 2008), but this is by no means universal in congeneric comparisons (Kloeppel and Abrams 1995; McDowell 2002; Gerlach and Rice 2003), nor in analyses of regional floras (Hamilton et al. 2005; Leishman et al. 2007).

Dry matter content can be viewed as a stand-in for leaf density, one of the components of LMA, along with leaf thickness (Shipley and Vu 2002). Low leaf density may have a salutary effect on growth rate because dense leaves present more of an internal barrier to the diffusion of CO_2 or the penetration of light to chloroplasts, or because the construction cost of such a leaf is higher (Niinemets and Sack 2006). Several studies have attributed invasive success partly to lower construction costs, including several where the comparison was between invasive and non-invasive congeners (Pammenter et al. 1986; Deng et al. 2004). An ordination of 16 traits measured in a group of woody vines suggested that the major axis

dividing natives from invasives was LMA and leaf construction costs, which were significantly linked with RGR. However, in an analysis of 29 species of pines, Grotkopp and colleagues (2002) found that neither leaf thickness or density was associated with invasiveness; rather, a developmental aspect of LMA, the rate of leaf production, was higher in invasive than non-invasive species.

Resource capture and efficiency

Leaf-level nutrient content differed little between invaders and non-invaders. Non-invasive species had higher phosphorus content in leaves, which could indicate superior ability to take up that nutrient from the soil. However, non-invasive species had significantly higher leaf percentage P at the time of transplant into the low-nutrient treatment (Matzek, unpublished data), when seedlings were only about a week old and had not yet been fertilized, and so this trait is likely an artifact of the starting conditions. Otherwise, leaves in both groups did not vary significantly in nitrogen, chlorophyll, or protein content.

Invasive species were, however, significantly more efficient with regard to nitrogen-use in photosynthesis. Interspecific variation in photosynthetic nitrogen-use efficiency (PNUE) may result from differences in the way plants allocate nitrogen within the cell. A number of studies have found higher PNUE associated with greater investment of N in the photosynthetic apparatus or lower allocation to cell-wall structural proteins (Hikosaka et al. 1998; Ripullone et al. 2003; Westbeek et al. 1999; Onoda et al. 2004; Takashima et al. 2004). Woody evergreens may use Rubisco as a storage protein, further diminishing PNUE (Warren et al. 2000; Warren and Adams 2001, 2002; Warren et al. 2003). The oft-observed association between low LMA and high PNUE suggests that plants with high LMA have thicker cell walls, lower g_i and C_c and consequently lower PNUE (Hikosaka 2004; Warren and Adams 2004). Among congeneric invasive-non-invasive pairs, Feng and colleagues (2008) found that PNUE and the fraction of N allocated to bioenergetics and carboxylation were all significantly correlated with SLA. It is important to note that the present study, which measures instantaneous PNUE on seedlings, cannot account for variation in leaf lifespan between invasives and non-invasives. Higher LMA leaves should also persist longer on the plant, and therefore the integrated (lifelong) PNUE of a non-invasive leaf may equal or exceed that of an invasive leaf. Under low-resource conditions in Hawaii, Funk and Vitousek (2007) found that instantaneous efficiency measures were typically higher in the invasive species, but that this difference evened out when the longer leaf lifespan of native species was accounted for.

Efficiency with regard to nitrogen-use did not extend to water-use. Non-invaders had significantly higher WUE. A tradeoff between PNUE and WUE may result if plants increase stomatal conductance to raise the intercellular concentration of CO_2, because photosynthesis will then increase with no change in nitrogen content but with an increase in diffusion of water out of the leaf (Field et al. 1983; Reich et al. 1989). In observing a negative correlation between WUE and NUE across a range of water-limited and N-limited treatments in spruce, where greater WUE was associated with droughtier conditions and greater NUE associated with nutrient scarcity, Patterson and colleagues (1997) suggested that species plastically optimize use-efficiency of the most limiting local resource. However, in this study, water was not limiting to plant growth, so it is not certain that these water-use efficiency patterns among invasives and non-invasives would be observed in drought conditions. Moreover, a tradeoff between these traits is not universal. McDowell (2002) found that invasive members of the genus *Rubus* had higher rates of photosynthetic capacity for lower investments of leaf resources, including both higher instantaneous NUE and instantaneous WUE, than non-invasive congeners. In a series of studies of congeneric pairs of species where NUE was consistently shown to be higher in the invasive member of the pair, higher WUE was sometimes associated with the invader and sometimes with the non-invader (Feng et al. 2008).

Neither group of pines showed greater efficiency at acquiring nutrients from the soil. Per unit root mass, uptake of nitrogen (SAR_N) and phosphorus (SAR_P) were indistinguishable. Higher uptake efficiency may help invaders exploit nutrient-rich microsites better than native competitors, and contribute to the speed of their colonization in a new area. The invasive forb *C. maculosa* was found to have higher N uptake efficiency relative to two native grass competitors, but

there may be no long-term advantage to this strategy, as natives allocated more overall root mass and had similar total N absorption (Blicker et al. 2002). In this study, there is no measure of root morphology, analogous to the LMA for the leaves, to judge whether invasive and non-invasive roots differed in their length or surface area extent per unit mass. Measurements of the specific-root-length, or root length per unit mass, have sometimes been correlated with RGR (Reich et al. 1998), but I know of no studies that have compared this trait between invasive and non-invasive groups of species.

In sum, this research does not support the idea of a single general syndrome of invasiveness, whereby invaders are exploitative and non-invaders are patient; or where invaders are profligate and non-invaders efficient. Instead, the finding that differences in performance were correlated to invaders' superior nutrient-use efficiency and non-invasives superior water-use efficiency, with both these traits linked to morphological differences in LMA, leads to a conclusion that traits that confer fitness in a particular resource context matter most to invasiveness. In the present case, invaders may allocate leaf nitrogen more efficiently to maximize photosynthesis and growth in nitrogen-poor soils, while non-invaders with more heavily defended leaves may have an advantage in drier areas. Context-dependence may apply to other traits, too; small seed size, linked to invasiveness in pines by Rejmánek and Richardson (1996), may be associated with fast growth in a wetter climate but be disadvantageous to establishment in an arid climate. From a study of 122 invasive and native species in eastern Australia, Leishman et al. (2010) concluded that invasives did not have fundamentally different carbon capture strategies from natives, but had higher values for traits like photosynthetic rate and nitrogen content that promoted their capacity for growth in disturbed areas. Muth and Pigliucci (2006) have argued cogently that the lack of consistently shared attributes across phylogenetically comparable invasive and non-invasive species should not be grounds for dismissing the usefulness of traits in predicting invasiveness, but rather that meaningful combinations of traits in particular local contexts results in invasion.

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