

A test for a cost of opportunism in invasive species in the Commelinaceae

Jean H. Burns · Stacey L. Halpern
Alice A. Winn

Received: 1 September 2005 / Accepted: 23 May 2006 / Published online: 29 November 2006
© Springer Science+Business Media B.V. 2006

Abstract Many invasive species can respond opportunistically to favorable growing conditions. In a previous work, we found that invasive species in the family Commelinaceae were more opportunistic than their noninvasive congeners and could therefore outperform noninvasive relatives in an environment with abundant resources and no competition. Contrary to the expectation that superior performance under favorable conditions comes at the cost of reduced performance under stressful conditions, invasive species did not perform more poorly relative to noninvasive congeners under any conditions we examined. Here we expand our search for potential costs of opportunism in invasive species to additional environmental conditions in which invasive taxa have been shown or predicted to perform poorly. We grew four invasive and four noninvasive species in environments consisting of all possible combinations of high and low soil resources and presence and absence of clipping (removal of aboveground biomass). We also fed leaves of

each species to a generalist herbivore to assess resistance to herbivory. We found that the advantage of invasive species is reduced but not eliminated by low soil resources and clipping. At low soil resources, invasive species produced softer leaves than noninvasive species and might therefore be less resistant to generalist herbivory than noninvasive species, although a direct comparison of resistance in a no-choice bioassay revealed no difference. The invasive species outperformed noninvasive species only under the most favorable conditions, and the noninvasive species did not outperform the invasive species in any environment.

Keywords Clipping · Commelinaceae · Herbivore resistance · Invasive plants · Opportunism · Relative growth rate · Root-to-shoot ratio · Soil nutrients · Specific leaf area

Introduction

Invasive plants are a major source of worldwide economic and ecological disruption, causing loss of species, altering community composition, and affecting ecosystem processes (see, e.g., Vitousek et al. 1996; Perrings et al. 2000). However, not all introduced species become problematic invaders (see, e.g., Rejmánek and Richardson 1996).

J. H. Burns (✉) · A. A. Winn
Department of Biological Science, Florida State University, Tallahassee, FL 32306-1100, USA
e-mail: burns@bio.fsu.edu

Present Address:
S. L. Halpern
Biology Department, Pacific University,
2043 College Way, Forest Grove, OR 97116, USA

Previous studies have shown that traits of both species and environments can influence the likelihood of success and the consequences of invasion (Daehler and Carino 2000; Daehler 2003). Because invasive species often have a performance advantage only in more favorable environments (reviewed by Daehler 2003), specialization for exploiting productive environments could be common among invasive plant species.

High growth rate in favorable environments is associated with poor performance in more stressful environments across a range of plant taxa (Chapin 1980; Lambers and Poorter 1992; Chapin et al. 1993), indicating that specialization on productive environments may come at the cost of poor performance under poorer conditions. Consistent with the notion that opportunistic invasive species may pay a cost of reduced ability to persist in more stressful habitats, invasives are reported to be less successful in habitats characterized by abiotic stress and some kinds of disturbance (reviewed by Daehler 2003). Although disturbance per se often favors invasive species over natives (Caldwell et al. 1981; Burke and Grime 1996; Daehler 2003), some forms of natural disturbance including fire and flooding may reduce the advantage of invasive species (reviewed by Hobbs and Huenneke 1992; Daehler 2003). For example, Baruch and Bilbao (1999) found that an invasive Hawaiian grass was affected more by fire than was a native Venezuelan grass and suggested that lower tolerance of fire could be a cost associated with the high potential growth rate of the invasive species. Invasive species may also be less likely to have an advantage in environments characterized by strong abiotic stress such as drought or high salinity (reviewed by Daehler 2003). A possible interpretation of these patterns is that, in favorable environments, rapid growth confers an advantage and that invasive species possess traits that make them fast growers. Under more stressful conditions, species with adaptations that alleviate the effects of stress at the cost of the ability to grow fast may have an advantage (Chapin et al. 1993; Arendt 1997; but see Fernández and Reynolds 2000).

One way that invasive species might achieve high growth rates in undisturbed environments is through disproportionate allocation to above-

ground tissue. This pattern could place them at a disadvantage relative to species with greater allocation to belowground tissue in environments in which disturbance, such as mowing, grazing, or burning, removes aboveground tissue only. Such disturbance should favor species that are best able to survive the initial disturbance and then to replace photosynthetic tissue. Underground tissue could provide the resources required to support compensatory growth after disturbance, but all else being equal, increased investment in non-photosynthetic tissue would be expected to reduce growth rate (Chapin 1980; Korner 1991). Greater allocation to belowground tissue would also be expected to promote growth in environments in which the availability of belowground resources limits growth (Chapin 1980; Lambers and Poorter 1992). Additional traits such as thick, durable leaves that promote the efficient use of water and nutrients, but often at the cost of reduced photosynthetic rate, should also confer an advantage in low-productivity habitats (Lambers and Poorter 1992; Barrett 2000). If invasive species specialize on environments with limited abiotic stress and minimal loss of aboveground tissue, we might expect them to have lower root-to-shoot ratios and thinner leaves than noninvasive species.

Herbivores may also influence the success of invasive species. The enemy-escape hypothesis posits that invasive species leave their specialist herbivores behind when they invade a foreign range, thereby gaining an advantage over native species, which must cope with their specialist herbivores while competing against the herbivore-free invaders (reviewed by Maron and Vilá 2001; Keane and Crawley 2002; but see Colautti et al. 2004). On the other hand, an association between invasiveness and high growth rate could also make invasive species inherently more susceptible to herbivores, including generalists, because traits that confer resistance to herbivory often reduce growth rate (reviewed by Bergelson and Purrington 1996; Strauss et al. 2002). For example, thin leaves are associated with higher growth rates, but herbivores often prefer thin, poorly defended leaves over thick, tough ones (Feeny 1970; Coley 1983).

In previous work, we found that a group of invasive species in the Commelinaceae performed

better than their noninvasive relatives in environments that lack competitors (Burns and Winn 2006) and those with either abundant soil nutrients or water (Burns 2004). In contrast to the expectation that superior performance in high quality environments comes at the cost of reduced performance under more stressful conditions, we found no difference in the performance of invasive and noninvasive species in the presence of competitors (Burns and Winn 2006) or in water- or nutrient-limited conditions (Burns 2004). Here we examine additional stressful environmental conditions that have been suggested or demonstrated to favor noninvasive relative to invasive species including disturbance, extreme abiotic stress, and the effects of herbivory. Specifically, we test the hypotheses that, compared to noninvasive species, invasive species (a) suffer disproportionately in response to disturbance that removes aboveground biomass, (b) are more sensitive to the combination of reduced water and nutrients, and (c) are less resistant to a generalist herbivore. We also sought to determine whether invasive species exhibit traits typically associated with rapid growth in productive environments, including greater positive responses to increased resource availability (i.e., greater opportunism); greater specific leaf area; smaller, less tough leaves; and lower ratio of root to shoot biomass.

Materials and methods

The Commelinaceae are a species-rich family with numerous weedy or invasive members, including some pest plants that pose serious management problems (Holm et al. 1977; Wilson 1981; Faden 1982; Standish et al. 2001). We previously compared the traits and plastic responses to competition of four species in this family that have been designated invasive in North America (*Commelina benghalensis*, *Murdannia nudiflora*, *Tradescantia fluminensis*, and *T. zebrina*) with those of four congeners that have been introduced into North America but have not been identified as invasive (*C. bracteosa*, *M. simplex*, *T. blossfeldiana*, and *T. brevifolia*). Invasive species were defined as nonnative species that have

spread rapidly (Richardson et al. 2000), and were identified according to published invasive species lists (e.g., USDA 2002). Our previous documentation of significant phenotypic differences between the invasive and noninvasive species (Burns 2004, Burns and Winn in press) suggests that these categories are biologically meaningful, though we cannot rule out the possibility that noninvasive species will become problematic invaders in the future.

In the study reported here, we used the same eight species as in previous work (Burns and Winn 2006). Due to the limited availability of live material for some species, each species was represented by a single genotype and thus species is the unit of replication for the comparison of invasive and noninvasive taxa (cf. Burns and Winn 2006). Previous work with the same set of genotypes has successfully identified consistent differences between these invasive and noninvasive taxa despite limited within-species sampling (Burns and Winn 2006).

Performance in low-quality environments and in response to disturbance

Individuals of all eight species were planted as cuttings, each consisting of two leaves and one leafless, buried node, in the greenhouse as in Burns (2004) and Burns and Winn (2006). Each cutting was planted alone in a pot (1570 cm³) filled with a 2:1 mixture of sand to potting mix. We manipulated environmental quality (high/low) and removal of aboveground tissue (clipping/no clipping) in a factorial design. Plants in the high-quality environment received ample water (the soil was kept damp, and plants were not allowed to wilt) and were fertilized approximately every 3 weeks at the recommended application rate (Peters special 20-20-20 at 2.4 g/l). Plants in the low-quality environment were watered only after they appeared stressed (i.e., wilted) and were not fertilized at all. Twenty replicate cuttings of each species were grown in each clipping treatment in the low-quality environment and 10 replicates per clipping treatment were grown in the high-quality environment (480 plants total). Greater replication in the low-quality environment was meant to assure

adequate sample sizes in the face of greater expected mortality.

After the plants had grown for 23–30 d in the high-quality environment and 45–47 d in the low-quality environment, we clipped off and removed all aboveground biomass except the two most basal leaves from plants in the clipping treatments. This treatment was imposed by clipping the main stem of each individual just above the two most basal leaves with scissors. In all cases, clipping was not imposed until more than two leaves were available to clip. Because plants grew at different rates, depending on species and environment, we imposed the clipping treatment at different times for different pairs of congeners in different treatments and harvested the high-quality treatment before the low-quality treatment.

Plants in the high-quality treatments were harvested on 16 July 2004, after 55 days of growth, and plants in the low-quality treatment were harvested on 12 August 2004, after 81 days of growth. The longer period for growth for plants in the low-quality environment will bias against detecting differences in overall growth between high- and low-quality environments, but will not affect the comparison of invasive with noninvasive taxa within an environment, which is our primary focus. Harvested plants were separated into root and shoot tissue, dried at 55°C, and weighed to the nearest 0.001 g.

Final plant size (dry biomass of all tissue) was our measure of performance. Final biomass after clipping (not including biomass removed in the clipping treatment) was our estimate of compensatory growth. Plasticity in performance in response to clipping was estimated for each species as the difference between the mean biomass of plants in the clipped and unclipped treatments within an environmental quality treatment, and plasticity in response to environmental quality was estimated as the difference between mean biomass in high- and low-quality environments within a clipping treatment.

Resistance to herbivores

To estimate resistance to a generalist herbivore, we measured the relative growth rates of larvae of

Spodoptera frugiperda (Lepidoptera: Noctuidae) that were offered leaves of each species from each soil-resource environment in no-choice feeding trials. *Spodoptera frugiperda* is a polyphagous agricultural pest reported to feed on more than 80 species, although its preferred hosts are grasses (reviewed by Sparks 1979; Capinera 1999). After briefly starving second- and third-instar larvae to clear their guts, we weighed them individually and placed each one in a plastic cup (29.6 ml soufflé cups, Solo Cup Company, Urbana, IL, USA) with damp filter paper and excised leaves from a single species grown in one environment (high or low quality). Larvae fed for two days in an environmental chamber (27°C, 16L:8D, Percival E36L, Perry, IA, USA) before they were again briefly starved and then reweighed. The experiment initially included 6–10 larvae for each species in each environment (total $n = 119$); 3–8 larvae survived in each species–environment combination (total $n = 104$).

We calculated larval relative growth rate (RGR) as $[\ln(\text{final mass}) - \ln(\text{initial mass})]/\text{days of growth}$. Because greater larval RGR indicates lower plant resistance, we used the difference between the maximum observed larval RGR and the RGR for each larva as our measure of resistance. From the plant perspective, an important component of resistance is amount of leaf damage. Although larval RGR incorporates both consumption (i.e., amount of damage) and assimilation (i.e., efficiency of conversion of plant biomass consumed to herbivore biomass), the area of leaf consumed and larval RGR were positively correlated (Spearman rank correlation, $r = 0.41$, $P = 0.01$ for a subset of 40 replicates from the low-quality treatment for which both variables were estimated).

When it was available, we used clipped material for feeding trials. We also sacrificed up to three individuals per species in the low-quality treatment to provide adequate tissue for larval feeding trials. These individuals were excluded from all subsequent analyses.

Traits associated with invasiveness

To determine if traits associated with high growth rate are also associated with invasiveness in the

Commelinaceae, we measured or calculated a set of additional traits of our experimental plants, including the ratio of final root dry biomass to shoot dry biomass (root-to-shoot ratio), relative growth rate (RGR) for unclipped plants and regrowth rate for clipped plants, leaf size (leaf dry biomass), specific leaf area (SLA = leaf area/leaf dry biomass), and leaf toughness. For unclipped plants, RGR is the difference between the natural log of final total biomass and the natural log of initial biomass divided by the number of days the plant grew. Because plants in the clipped treatments were reduced to the approximate above-ground size of the original cuttings (two leaves), we estimated relative regrowth rate in the clipped treatment as the difference between log of final biomass and log of initial estimated biomass of the original cutting divided by the number of days from clipping to harvest. This procedure does not accurately estimate RGR because it does not take into account root biomass at the time of clipping, but it does reflect the relative rates at which plants recovered from clipping.

To determine SLA and leaf size for all plants, we collected the most recent fully expanded leaf from each individual regardless of treatment at the time when clipping was imposed. After measuring leaf area with a leaf-area meter (CI-201, CID, Inc., 4845 NW Camas Meadows Drive, Camas, WA, USA), we dried and weighed individual leaves. We used a penetrometer to measure leaf toughness as the mass of sand necessary to push a nail through the leaf (Feeny 1970).

Data analysis

To determine whether treatments and their interactions influenced plant performance or trait expression, we performed ANOVA for the effects of environmental quality, clipping, species, and their interactions on whole-plant traits. The effect of species was included to account for expected variation among species, but is not interpreted because we are interested in differences between invasive and noninvasive taxa rather than among all species. The effects of clipping were not included in the analysis of leaf traits or herbivore resistance because leaves were collected and measured only once, when

clipping treatments were imposed. All factors were treated as fixed effects, and we used Type III sums of squares to calculate mean squares because sample sizes were unequal. Data were transformed as necessary to meet the assumptions of ANOVA (Sokal and Rohlf 1981). Post-hoc comparisons of treatment means were performed by the Tukey–Kramer method (Sokal and Rohlf 1981).

To homogenize variances, we took the natural logs of specific leaf area and resistance and the square root of leaf toughness. One estimate of resistance was an extreme outlier because the larva lost about half of its mass between the initial and final weighing (four times more than any other larva), indicating either imminent death or measurement error. We excluded this datum from the analysis. Total dry biomass was natural-log transformed before analysis, but very large treatment effects for this variable made homogenization of the variances impossible. Significance tests involving this variable should therefore be viewed as approximate.

Because species differed in the initial size of the cutting that was planted, we included estimated initial cutting mass as a covariate in the analysis of final biomass (cf. Burns and Winn 2006). Initial cutting mass was estimated from regressions of cutting dry biomass on linear measurements of cutting size (cutting length and leaf width and length for each of 2 leaves) for 30 cuttings per species. Consistent with the assumptions required for ANCOVA, the species-by-initial-biomass interaction did not explain a significant amount of variation in total final biomass ($F = 1.02$, $P = 0.4141$).

We paired each invasive species with its most closely related noninvasive congener and conducted paired t -tests to examine differences in the traits of invasive and noninvasive species controlling for relatedness (Felsenstein 1985, Harvey and Pagel 1991). Each invasive *Tradescantia* species was paired with the congener more closely related to it on the basis of a preliminary molecular phylogeny (J.H.B., unpublished data).

We also used paired t -tests to compare the plasticity of final biomass for invasive and noninvasive species. Plasticity was quantified as the difference between the mean final biomass in two

environments for each species (cf. Burns and Winn 2006).

The ANOVAs were conducted with the GLM procedure and paired *t*-tests with PROC T-Test in SAS Ver. 8.01 (SAS Institute 1999). Means are reported as backtransformed values with backtransformed standard errors (Sokal and Rohlf 1981).

Results

Of 480 plants, 10 died during the experiment, from 0 to 2 out of 60 individuals of each of the 8 species. At least 16 individuals per treatment combination remained to be harvested in the low-quality treatment, and at least 9 survived in the high-quality environment. On average, cuttings grew to more than 20 times their initial size over the course of the experiment (mean estimated initial dry biomass of cuttings 0.093 g, mean final dry biomass 2.07 g).

Differences among environments

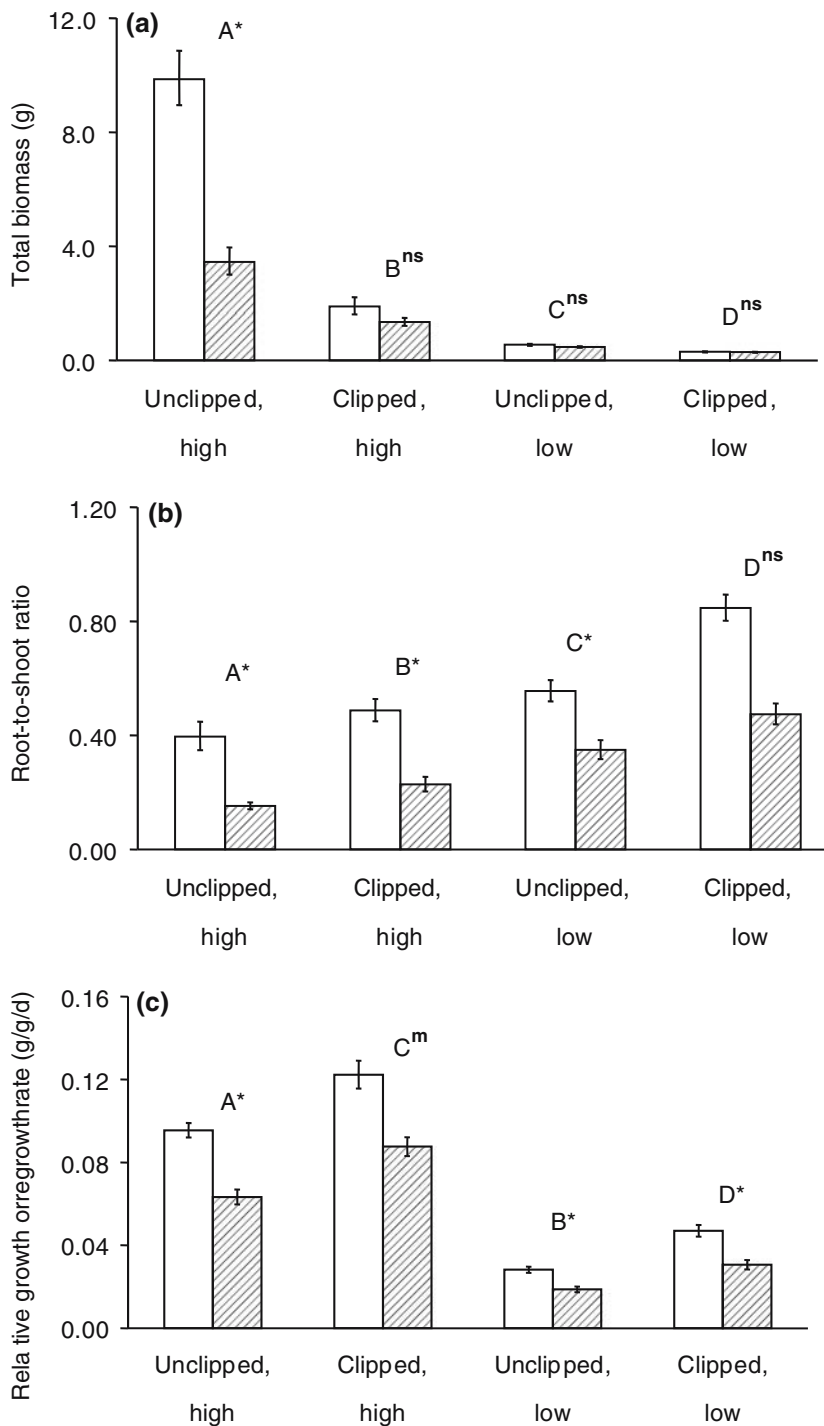
Not surprisingly, the four environments differed substantially in mean final biomass, ranging from a mean of 5.83 g for the high-quality, unclipped environment to a mean of 0.29 g for the low-quality, clipped environment (Fig. 1a). Final biomass was significantly greater on average in the high-quality environments (Table 1) despite the longer growth period for plants grown in the low-quality environments (high-quality mean 3.05 g, low-quality mean 0.38 g). Final biomass was also significantly greater in unclipped environments (unclipped mean 1.21 g, clipped mean 0.52 g). Mean root:shoot also differed significantly among all four environments (Table 1, Fig. 1b) in a pattern opposite to that for total final biomass; as total final biomass decreased, root:shoot increased (Fig. 1a, b). Mean relative growth rate was significantly greater in the high-quality than low-quality unclipped environment, and mean regrowth rate was greater in the high-quality clipped than the low-quality clipped environment (Table 2, Fig. 1c). Leaves produced in the high-quality environment were significantly heavier and less tough than those produced in the

Fig. 1 Trait means (backtransformed \pm SE) for four invasive (open bars) and four noninvasive (hatched bars) species grown in high- and low-quality environments and either clipped (i.e., subjected to removal of aboveground biomass) or not clipped: total dry biomass at harvest (a), root-to-shoot ratio (b), relative growth rate (RGR) for plants in the unclipped treatments and relative regrowth rate for plants in the clipped treatments (c). Uppercase letters designate differences between environment means (without respect to invasiveness). Means that share letters are not statistically significantly different on the basis of Tukey–Kramer post-hoc tests across all environments for (a) and (c). Relative growth rate and regrowth rate were compared within clipping treatments only (A, B for unclipped plants and C, D for clipped plants). Asterisks denote a significant difference in the mean of invasive versus noninvasive species within an environment based on paired *t*-tests, $m = 0.05 < P < 0.10$, ns = $P > 0.10$

low-quality environment, but there was no difference in specific leaf area (Table 3, Fig. 2a–c).

Comparison of invasive and noninvasive species

On average, invasive species produced greater final biomass than noninvasive species (invasive mean 0.91 g, noninvasive mean 0.67 g), but paired *t*-tests indicated that total final biomass was significantly greater for invasive than noninvasive species only in the most productive environment (Table 4, Fig. 1a). Invasive species were also somewhat larger at harvest in the high-quality, clipped and low-quality, unclipped treatments, but these differences were not statistically significant (Fig. 1a). The absence of significant differences between the final sizes of invasive and noninvasive species in the clipped environments (Table 4, Fig. 1a) indicates no difference in compensatory growth. Invasive species had a greater positive plastic response of total final biomass to the high-quality environment than did noninvasive species when both were unclipped (paired $t = 2.58$, $P < 0.05$). The same trend was apparent for clipped plants (Fig. 1a) but was not significant (paired $t = 1.22$, $P > 0.10$). Invasive species also responded more positively to the absence of clipping. In the high-quality environment, plasticity in final biomass in response to clipping was significantly greater for invasive than for noninvasive species (paired $t = 2.78$, $P < 0.05$). The pattern of response was similar in



the low-quality environment, although the difference between invasive and noninvasive species was not significant (paired $t = 0.64$, $P > 0.10$).

Invasive and noninvasive species differed in both whole-plant and leaf traits, although some

differences depended on the environment in which plants were grown. Invasive species had significantly greater root-to-shoot ratio than noninvasive species in all environments except the low quality, clipped environment (Table 4,

Table 1 ANOVA for the effects of species, environment quality, and clipping on total dry biomass at harvest and on the ratio of root dry biomass to shoot dry biomass (root-to-

shoot ratio) in four invasive species and four introduced but noninvasive congeners in the Commelinaceae

Source	Total biomass			Root-to-shoot ratio		
	df	MS	<i>F</i>	df	MS	<i>F</i>
Initial cutting weight	1	2.5	17***	NA	NA	NA
Species (S)	7	14	94***	7	12.6	44***
Quality (Q)	1	433	2870***	1	39	138***
Clipping (C)	1	86	573***	1	11	40***
S × Q	7	5.5	36***	7	1.5	5.2***
S × C	7	1.3	8.4***	7	0.93	3.3**
Q × C	7	14	96***	7	0.02	0.08
S × Q × C	7	0.74	4.9***	7	0.63	2.2*
Error	417	0.15		416	0.28	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ **Table 2** ANOVA for the effects of species and environmental quality on relative growth rate (RGR) of unclipped plants and on relative regrowth rate of clipped

plants for four invasive species and four introduced but noninvasive congeners in the Commelinaceae

Source	RGR			Relative regrowth rate		
	df	MS	<i>F</i>	df	MS	<i>F</i>
Species (S)	7	0.04	99***	7	0.07	79***
Quality (Q)	1	0.81	1810***	1	0.87	946***
S × Q	7	0.002	6.4***	7	0.007	7.9***
Error	200	0.12		213	0.001	

* $P < 0.05$, *** $P < 0.001$ **Table 3** ANOVA for the effects of invasiveness and environment quality on leaf toughness, specific leaf area (leaf area/leaf dry biomass), and leaf dry biomass for four

invasive species and four introduced but noninvasive congeners in the Commelinaceae

Source	Leaf toughness			Specific leaf area			Leaf weight		
	df	MS	<i>F</i>	df	MS	<i>F</i>	df	MS	<i>F</i>
Species (S)	7	138	43***	7	2.4	77***	7	2.2	106***
Quality (Q)	1	523	161***	1	0.11	3.4 [†]	1	3.6	172***
S × Q	7	19	5.8***	7	0.44	14***	7	0.23	11**
Error	148	3.2		348	0.03		420	0.02	

[†] $P < 0.10$, ** $P < 0.01$, *** $P < 0.001$

Fig. 1b). Invasive species had significantly greater RGR and relative regrowth rate than noninvasive species in all environments, though the difference was only marginally significant in the high quality, clipped environment (Table 4, Fig. 1c). Noninvasive species had significantly tougher leaves than invasive species in the low-quality treatment (Table 5, Fig. 2a). Consistent with their greater

toughness, the noninvasive species also had thicker leaves (lower SLA) than invasive species, though this difference was only marginally significant in both environments (Table 5, Fig. 2b). Leaf weight was greater on average for the noninvasive species than for the invasive species in both environments (Fig. 2c), but the differences were not statistically significant (Table 5, Fig. 2c).

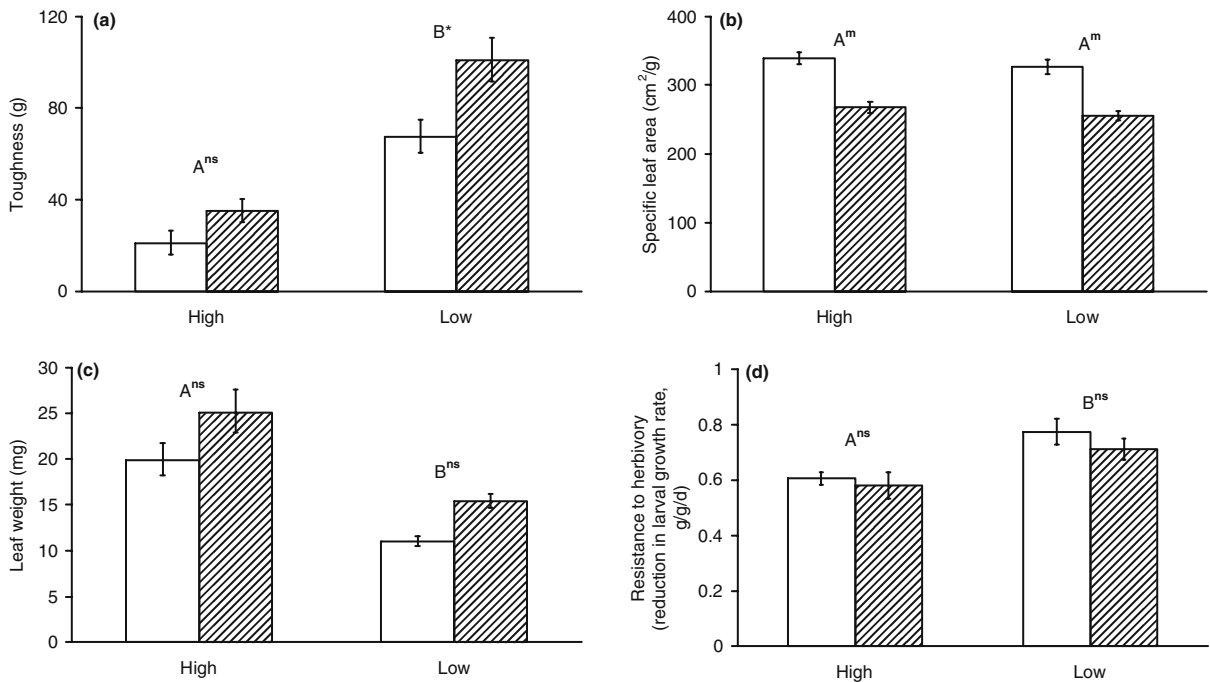


Fig. 2 Mean (\pm SE) leaf toughness (a), specific leaf area (SLA) (b), leaf weight (c), and resistance to herbivory by larval *Spodoptera frugiperda* (measured as the difference in larval growth rate between the maximum observed larval RGR and the RGR for each larva) (d) for invasive (open bars) and noninvasive (hatched bars) species grown in high- and low-quality environments.

Uppercase letters designate differences between environment means (without respect to invasiveness). Means that share a letter are not significantly different. Asterisks denote a significant difference in the mean of invasive versus noninvasive species within an environment based on paired *t*-tests, $m = 0.05 < P < 0.10$, $ns = P > 0.10$

Resistance to herbivory

Of 118 *Spodoptera frugiperda* larvae in the resistance experiment, 88% survived, and 86% consumed at least some leaf tissue during the feeding trial. On average, larval RGR was 0.21 mg/day (range -0.14 to 0.88 mg/day), and 81% of surviving larvae gained weight over the 2-day trial.

Spodoptera frugiperda growth rate varied significantly with plant growing conditions (environmental quality) ($F_{1,87} = 24.4$, $P < 0.001$), plant species ($F_{7,87} = 6.82$, $P < 0.01$), and the interaction between these factors ($F_{7,87} = 3.45$, $P < 0.01$). *Spodoptera frugiperda* larvae raised on plants from the low-quality environment grew about 30% less than those raised on high-quality environment plants (Fig. 2d). Larval growth rate did not differ on invasive and noninvasive species on average or within either environment quality (Table 5, Fig. 2d).

Discussion

We confirmed that invasive species outperform noninvasive species only in the environment most favorable for growth. We found no conditions under which noninvasive species performed better than invasive species, although lower leaf toughness suggests the possibility that invasive species would be more susceptible to herbivory under more stressful conditions. A syndrome of traits including high RGR, high root-to-shoot ratio, and the production of thin, soft leaves was associated with invasiveness.

The cost of invasiveness

Consistent with previous experiments with the same set of species grown under different environmental conditions (Burns 2004, Burns and Winn 2006), invasive species responded more

Table 4 Paired *t*-tests comparing mean total biomass, root-to-shoot ratio, and relative growth (or regrowth) rate for four invasive and four noninvasive species in the Commelinaceae in four environments including all combinations of high and low quality and clipping treatments (clipped and unclipped plants)

Trait	<i>t</i> -value	<i>P</i> -value
<i>Environment</i>		
Final plant biomass (g)		
High unclipped	2.51	0.044
Low unclipped	0.60	0.29
High clipped	1.16	0.16
Low clipped	0.05	0.48
Root-to-shoot ratio		
High unclipped	2.58	0.04
Low unclipped	3.65	0.02
High clipped	2.55	0.04
Low clipped	1.46	0.12
Relative Growth Rate (ln(g)/ln(g)/d)		
High unclipped	3.03	0.028
Low unclipped	3.23	0.024
High clipped	1.76	0.089
Low clipped	2.73	0.036

Sample size is four for all comparisons

opportunistically to higher-quality environments, including both greater availability of soil resources and the absence of clipping, as indicated by their greater plasticity in total final biomass. The performances of invasive and noninvasive species were most similar in the most stressful environment, the low-quality, clipped treatment (Fig. 1a).

We found no evidence for several potential costs to the greater performance of invasive species in better environments. First, the failure of noninvasive species to outperform invasive species in either clipping treatment (Table 4, Fig. 1a) indicates that they do not have greater compensatory growth than invasive species. Although invasive species were not significantly larger than noninvasive species in our clipped treatments, their greater relative regrowth rates (Table 4, Fig. 1c) suggest that, given more time, the invasive species would eventually have exhibited greater compensation than noninvasive species. Our results are therefore not consistent with the hypothesis that poorer response to aboveground disturbance is a cost of invasiveness. The greater root-to-shoot ratio we observed in invasive than in noninvasive species (Fig. 1b) could be a

Table 5 Paired *t*-tests comparing trait means of four invasive and four noninvasive species in the Commelinaceae in high and low quality environments

Trait	<i>t</i> -value	<i>P</i> -value
<i>Environment</i>		
Leaf toughness (g)		
High	-0.44	0.34
Low	-6.01	0.005
Specific Leaf Area (cm ² /g)		
High	1.70	0.094
Low	1.81	0.084
Leaf weight (g)		
High	-0.39	0.36
Low	-0.67	0.28
Resistance (larRGR, ln(g)/ln(g)/d) ^a		
High	0.16	0.99
Low	0.67	0.55

Sample size is four for all comparisons. Because greater larval RGR indicates lower plant resistance, plant resistance to herbivory was measured as the difference between the maximum observed larval RGR and the RGR for individual *Spodoptera frugiperda* larvae raised on plants from both environmental growing conditions

^aTwo-way *t*-test, direction of trend opposite of predicted

mechanism conferring greater RGR and relative regrowth rates in the invasive species. Previous studies report greater compensatory growth of invasive species than of native species (e.g., Caldwell et al. 1981; Schierenbeck et al. 1994; Rogers and Siemann 2002). Ours appears to be the first comparison between invasive and introduced but noninvasive species, which is more appropriate for determining traits of invasive species because the invasion potential of native species is typically unknown.

Noninvasive species also did not exhibit greater tolerance of low soil resources, even when conditions severely limited growth. Lower tolerance of poor-quality environments therefore does not appear to be a cost of high performance in good-quality environments for these invasive species. Again, greater root-to-shoot ratio probably allowed invasive species to take up more soil resources.

A caveat to our conclusion that invasive species are not more tolerant of stressful environments is that mortality was uniformly low in our experiment. Although our treatments did create extremely stressful conditions, as judged by the nearly 20-fold difference in mean final biomass

among the treatments (Fig. 1a), we cannot rule out the possibility that conditions severe enough to inflict greater mortality would have revealed differential survival of invasive and noninvasive taxa. Greater survival by noninvasive species under such conditions would suggest increased mortality under stressful conditions as a cost of invasive species' better performance in good environments. Noninvasive species could also have an advantage at a life-cycle stage that we did not measure (cf. del-Val and Crawley 2005). For example, noninvasive species could have more successful seedling establishment under stressful conditions as a result of their slow growth, if growth rates tradeoff with survival (see, e.g., Grime and Hunt 1975).

Our direct test indicated no difference between invasive and noninvasive species in their resistance to feeding by *Spodoptera frugiperda* larvae, but the leaves of noninvasive species were significantly tougher on average than those of invasive species in the low-quality environment (Table 5, Fig. 2a). Greater leaf toughness has been associated with reduced herbivore damage in diverse systems (see, e.g., Feeny 1970; Coley 1983; but see Feller 1995), and herbivores may prefer to eat less tough leaves (Connor 1988). Herbivore selectivity in the field could lead to greater damage on the softer leaves of invasive species, which we could not detect in our no-choice measure of resistance. In support of the suggestion that herbivores might prefer to eat invasive taxa, grasshoppers showed similar consumption rates on genotypes of *Sapium sebiferum* from the native and introduced ranges in no-choice tests, but preferred genotypes from the introduced range when given a choice (Siemann and Rogers 2003). Similarly, Agrawal and Kotanen (2003) found that damage levels were greater on exotic than on native species in the field (but see Carpenter and Cappuccino 2005 for conflicting results) even though no-choice bioassays revealed no difference in resistance between the two types of plants.

Traits associated with invasiveness

We found that invasive species had greater relative growth rates than noninvasive species in most

environments (Fig. 1c), consistent with the results of other studies of relative growth rate in invasive species (Grotkopp et al. 2002; but see Bellingham et al. 2004). Our finding that invasive species have both greater root-to-shoot ratio and greater RGR and relative regrowth rate suggests that increased proportional allocation to nonphotosynthetic tissue does not necessarily come at the cost of RGR. The positive relationship we observed probably arose because light was not limiting in any of our environments and greater root-to-shoot ratio facilitated the uptake of soil resources, which were limiting growth.

We also found a trend towards greater SLA in invasive species (Fig. 2b), which is consistent with other studies (Pammenter et al. 1986; Baruch and Goldstein 1999; Durand and Goldstein 2001; Grotkopp et al. 2002). To our knowledge, leaf toughness has not been compared for invasive and noninvasive species in other studies. Our comparison provides support for a syndrome of leaf traits of invasive species, including high SLA and low toughness, which would be expected to maximize growth in productive environments.

Conclusions

Low soil resources and removal of aboveground biomass both decreased the performance advantage of invasive relative to noninvasive species in the Commelinaceae, but we found no conditions under which noninvasive species performed better than their invasive congeners. Greater RGR and root-to-shoot ratio, along with the production of thin, soft leaves, were generally associated with invasiveness. These traits could be used to predict invasiveness of proposed future introductions from this family and perhaps more broadly, but our results do not indicate any costs of being a good invader of productive habitats. The novel finding that noninvasive species have tougher leaves when soil resources are limited supports the possibility that invasive species are more susceptible to generalist folivores than are noninvasive species. Further investigation of resistance to herbivores in invasive species as a possible cost of opportunism would be valuable.

Acknowledgements We thank Roy Weidner for constructing our leaf penetrometer; Sarah Gray, Robin Hopkins, Ken Moriuchi, and three NSF Young Scholars Program students for assistance in harvesting 600 plants from wet sand under outrageously hot and humid conditions; Rob Meager for providing *Spodoptera frugiperda* eggs; and Nora Underwood for larval rearing advice and supplies. This manuscript was improved by comments from Katherine M. Howe, Thomas E. Miller, Anne B. Thistle, Nora Underwood, and two anonymous reviewers. Funds were provided by the Young Scholars Program, administered by the Office of Science Teaching Activities at Florida State University.

References

- Agrawal AA, Kotanen PM (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecol Lett* 6:712–715
- Arendt JD (1997) Adaptive intrinsic growth rate: an integration across taxa. *Q Rev Biol* 72:149–177
- Barrett PM (2000) Evolutionary consequences of dating the Yixian Formation. *Trends Ecol Evol* 15:99–103
- Baruch Z, Bilbao B (1999) Effects of fire and defoliation on the life history of native and invader C4 grasses in a Neotropical savanna. *Oecologia* 119:510–520
- Baruch Z, Goldstein G (1999) Leaf construction cost, nutrient concentration, and net CO₂ assimilation of native and invasive species in Hawaii. *Oecologia* 121:183–192
- Bellingham PJ, Duncan RP, Lee WG, Buxton RP (2004) Seedling growth rate and survival do not predict invasiveness in naturalized woody plants in New Zealand. *Oikos* 106:308–316
- Bergelson J, Purrington CB (1996) Surveying patterns in the cost of resistance in plants. *Am Nat* 148:536–558
- Burke MJW, Grime JP (1996) An experimental study of plant community invasibility. *Ecology* 77:776–790
- Burns JH (2004) A comparison of invasive and noninvasive dayflowers (Commelinaceae) across experimental nutrient and water gradients. *Divers Distrib* 10:387–397
- Burns JH, Winn AA (2006) Are invasive species more plastic? A comparison of plastic responses to competition by invasive and noninvasive congeners in the Commelinaceae. *Biol Invasions* 00:1–11
- Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS (1981) Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid Agropyron bunchgrasses. *Oecologia* 50:14–24
- Capinera JL (1999) Featured creatures: fall armyworm (*Spodoptera frugiperda*). University of Florida <http://www.creatures.ifas.ufl.edu/field/fall_armyworm.htm>. Accessed June 29, 2005
- Carpenter D, Cappuccino N (2005) Herbivory, time since introduction and the invasiveness of exotic plants. *J Ecol* 93:315–321
- Chapin FSI (1980) The mineral nutrition of wild plants. *Ann Rev Ecol Syst* 11:233–260
- Chapin FSI, Autman K, Pugnaire F (1993) Evolution of suites of traits in response to environmental stress. *Am Nat* 142:S78–S92
- Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecol Lett* 7:721–733
- Coley PD (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol Monogr* 53:209–233
- Connor EF (1988) Plant water deficits and insect responses: The preference of *Corythucha arcuata* (Heteroptera: Tingidae) for the foliage of white oak, *Quercus alba*. *Ecol Entomol* 13:375–381
- Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Ann Rev Ecol Syst* 34:183–211
- Daehler CC, Carino DA (2000) Predicting invasive plants: prospects for a general screening system based on current regional models. *Biol Invasions* 2:92–102
- del-Val E, Crawley MJ (2005) Are grazing increaser species better tolerators than decreasers? An experimental assessment of defoliation tolerance in eight British grassland species. *J Ecol* 93:1005–1016
- Durand LZ, Goldstein G (2001) Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. *Oecologia* 126:345–354
- Faden RB (1982) Commelinaceae. In: *Flora of North America* Editorial (ed) *Flora of North America*, Oxford University Press, New York, pp 170–197
- Feeny P (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565–581
- Feller IC (1995) Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecol Monogr* 65:477–505
- Felsenstein J (1985) Phylogenies and the comparative method. *The Am Nat* 125:1–15
- Fernández RJ, Reynolds JF (2000) Potential growth and drought tolerance of eight desert grasses: lack of a trade-off? *Oecologia* 123:90–98
- Grime JP, Hunt R (1975) Relative growth-rate: its range and adaptive significance in a local flora. *J Ecol* 63: 393–422
- Grotkopp E, Rejmánek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. *Am Nat* 159: 396–419
- Harvey PH, Pagel MD (1991) *The comparative method in evolutionary biology*. Oxford University Press Inc., New York, NY
- Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. *Conserv Biol* 6:324–337
- Holm LG, Plucknett DL, Pancho JV, Herberger JP (1977) Commelina. In: Holm LG, Plucknett DL, Pancho JV, Herberger JP (eds) *The world's worst weeds: distribution and biology*. Krieger Publishing Company, Honolulu, Hawai'i, pp 225–235

- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol Evol* 17:164–170
- Korner C (1991) Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. *Funct Ecol* 5:162–173
- Lambers H, Poorter H (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv Ecol Res* 23:187–261
- Maron JL, Vilá M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95:361–373
- Pammenter NW, Drennan PM, Smith VR (1986) Physiological and anatomical aspects of photosynthesis of two *Agrostis* species at a sub-Antarctic island. *New Phytol* 102:143–160
- Perrings C, Williamson M, Dalmazzone S (2000) Introduction. In: Perrings C, Williamson M, Dalmazzone S (eds) *The economics of biological invasions*. Edward Elgar, Cheltenham, UK, pp 1–13
- Rejmánek M, Richardson D (1996) What attributes make some plant species more invasive? *Ecology* 77:1655–1661
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concept and definitions. *Divers Distrib* 6:93–107
- Rogers WE, Siemann E (2002) Effects of simulated herbivory and resource availability on native and invasive exotic tree seedlings. *Basic Appl Ecol* 3:297–307
- SAS Institute I (1999) *SAS/STAT Users Guide*
- Schierenbeck KA, Mack RN, Sharitz RR (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology* 75:1661–1672
- Siemann E, Rogers WE (2003) Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. *Oecologia* 135:451–457
- Sokal RR, Rohlf FJ (1981) *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman, San Francisco, CA
- Sparks AN (1979) A review of the biology of the fall armyworm. *Fla Entomol* 62:82–87
- Standish RJ, Robertson AW, Williams PA (2001) The impact of an invasive weed *Tradescantia flumenensis* on native forest regeneration. *J Appl Ecol* 38:1253–1263
- Strauss SY, Rudgers JA, Lau JA, Irwin RE (2002) Direct and ecological costs of resistance to herbivory. *Trends Ecol Evol* 17:278–285
- USDA [United States Department of Agriculture] (2002) Animal Plant Health Inspection Service. Accessed online <<http://www.invasivespecies.gov>>
- Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. *Am Sci* 84:468–478
- Wilson AK (1981) *Commelinaceae: a review of the distribution, biology and control of the important weeds belonging to this family*. *Trop Pest Manage* 27:405–418