

Purple loosestrife suppresses plant species colonization far more than broad-leaved cattail: experimental evidence with plant community implications

Stephen M. Hovick^{1*†}, Daniel E. Bunker^{2‡}, Chris J. Peterson¹ and Walter P. Carson²

¹Department of Plant Biology, University of Georgia, 2502 Plant Sciences Building, Athens, GA 30602-7271, USA; and ²Department of Biological Sciences, University of Pittsburgh, 154A Crawford Hall, 4249 Fifth Avenue, Pittsburgh, PA 15260, USA

Summary

1. Dominant plant species, whether native or invasive, often change community composition and cause decreases in diversity. Still invasive species are considered more deleterious to communities than dominant natives, although evidence for this is surprisingly rare. We tested two hypotheses: (i) an exotic invasive species will have greater impacts at the community level than a dominant native and (ii) this deleterious impact will be exacerbated with eutrophication.

2. Both hypotheses were tested by evaluating colonizer success in large, well-replicated experimental monocultures of two dominant and widespread wetland species, invasive purple loosestrife (*Lythrum salicaria*) and native broad-leaved cattail (*Typha latifolia*). To facilitate comparisons, we standardized competitive effects by canopy biomass and by light availability beneath the canopy. The latter is a novel approach that accounts directly for resource reductions caused by community dominants.

3. Loosestrife was particularly detrimental to rare species and dramatically reduced colonizer success compared to cattail by nearly all of our metrics, including colonizer biomass (50.2% lower), species richness (34.2% lower), Shannon diversity (35.8% lower) and the proportion of mesocosms that were colonized (38.5% lower). Moreover, 15 of 16 uncommon species failed to colonize loosestrife communities. Graminoids fared poorly in loosestrife monocultures, but forb biomass (predominantly *Sagittaria latifolia*) was 3.5 times higher there. These results suggest that over time, plant communities under loosestrife canopies will contrast sharply with those under cattail. Contrary to our second hypothesis, fertilization did not exacerbate loosestrife's ability to suppress colonizers, relative to that of cattail.

4. Canopy biomass and light attenuation were similar for cattail and loosestrife, yet biomass explained little variation in colonizer success. Increasing light availability in the understorey increased colonizer richness and diversity only under cattail canopies, suggesting loosestrife suppresses colonization via below-ground competition while cattail does so via light reduction.

5. *Synthesis.* Ours is the first study to show that an invasive species suppresses colonizers much more than a dominant native and to identify contrasting mechanisms by which this may occur. Biomass-based comparisons of competitive effects may have limited utility for highly productive dominant species generally, thus our approach also offers a viable new alternative that could be applied broadly.

Key-words: Akaike's Information Criterion, competitive effect, light availability, *Lythrum salicaria*, model averaging, nitrogen enrichment, per-unit biomass, plant–plant interactions, root competition, *Typha latifolia*

*Correspondence author. E-mail: steve.hovick@gmail.com

Present addresses:

†Department of Ecology and Evolutionary Biology, Rice University, 6100 Main Street, Houston, TX 77005-1892, USA.

‡Department of Biological Sciences, New Jersey Institute of Technology, 433 Colton Hall, University Heights, Newark, NJ 07102, USA.

Introduction

Native and introduced species that regularly occur as community dominants often become so abundant that they displace or exclude co-occurring species, decrease biodiversity and alter community composition (Wisheu & Keddy 1992; Green & Galatowitsch 2002; Levine *et al.* 2003). Nutrient enrichment often enhances the abundance of dominant native and introduced plant species, exacerbating these community-level effects (Carson & Pickett 1990; Green & Galatowitsch 2002; Leishman & Thomson 2005). Both conventional wisdom and previous research suggest that invasive plant species (i.e. introduced dominants) cause greater declines in local diversity than their native counterparts and that nutrient enrichment disproportionately favours invasives (Daehler 2003; Leishman & Thomson 2005). This suggests dominant introduced species are better competitors than dominant natives, although most evidence for this comes either from correlative studies (Houlahan & Findlay 2004) or from experiments comparing invasives with native species that are locally uncommon or rare and thus likely to be weak competitors (Vilà & Weiner 2004; Vilà, Williamson & Lonsdale 2004).

To address this issue, we conducted an experiment to test whether the deleterious impacts incurred by a dominant introduced species on native communities were greater than impacts by a dominant native. We focused on impacts by the native broad-leaved cattail (*Typha latifolia* L.) and the invasive purple loosestrife (*Lythrum salicaria* L.), two ecologically important species that often occur as community dominants in temperate North American wetlands. Although both species can form dense, species-poor stands that seemingly resist invasion (Grace & Harrison 1986; Gabor, Haagsma & Murkin 1996), cattail is currently being displaced by loosestrife across much of North America (see 'Materials and Methods' section). Experimental evidence suggests loosestrife is a stronger competitor than most wetland species (Weiher *et al.* 1996), but this conclusion has been challenged by correlative studies that find either no relationship or a positive relationship between loosestrife abundance and species diversity in the field (Treberg & Husband 1999; Hager & Vinebrooke 2004).

Even more challenging than determining whether invasive species and ecologically similar dominant natives impact communities differentially is assessing whether their competitive effects are equal on a per-capita or per-unit biomass basis (Levine & D'Antonio 1999; Parker *et al.* 1999). For example, if loosestrife suppresses communities more than cattail does, it could be a stronger competitor on a per-amount basis (Goldberg & Werner 1983) or it may simply grow larger or more abundant (Gaudet & Keddy 1988). This distinction is rarely made (Parker *et al.* 1999; Vilà & Weiner 2004), but it is critical for understanding whether and how invasive species differ from native dominants in their impacts on native communities. We assess cattail and loosestrife competitiveness on a per-unit above-ground biomass basis here, and we also standardize their impact on the basis of light availability

beneath their canopies. In our system light is the resource most likely to limit colonizers, thus the better competitor may be the species that attenuates more light, regardless of its biomass.

Whether introduced or native, dominant species typically suppress colonization more with nutrient enrichment, at least partly because of increased productivity and concomitant light limitation to seedlings (Wisheu & Keddy 1992; Grace 1999; Hillebrand *et al.* 2007). Because wetlands are often nutrient rich, we expect above-ground competition to be particularly important in our study system. Below-ground competition may also increase with nutrient enrichment if dense roots prevent seedling establishment (Schenk, Callaway & Mahall 1999). In either case, the relationship between dominant species abundance and colonizer success may be nonlinear; for example, if dominant species at low abundance have weak effects on colonizers they may only suppress colonization above some productivity threshold (Schooler, McEvoy & Coombs 2006).

Colonizer success is also likely to depend on colonizer identity. Species that share traits relevant to their colonization ability may respond similarly to a given dominant species. Such similarity may also help identify mechanisms of colonizer suppression. For example, if a dominant species is shallow-rooted (as loosestrife is), deep-rooted colonizers that can reach soil resources not pre-empted by the resident dominant may be more successful (Berendse 1982; Fargione & Tilman 2005). Consequently, we evaluated whether forbs and graminoids differed in their colonization ability.

We addressed these issues by testing six predictions derived from two primary hypotheses: first, that the competitive effect of a dominant introduced species (loosestrife) will exceed that of a dominant native (cattail); and second, that this interspecific difference will be magnified at higher fertility. We tested our hypotheses by measuring establishment success at high and low fertility for 29 colonists within large replicated mesocosms containing monocultures of either cattail or loosestrife. We evaluated the degree to which canopy species identity, nitrogen availability, light availability, canopy biomass and their interactions explained colonization success. Specifically, we predicted that:

1. Colonizer success will be poorer under canopies of the invasive purple loosestrife than under the native broad-leaved cattail.
2. Increasing nitrogen fertilization will lower colonization overall, but it will do so to a greater extent under loosestrife than under cattail.
3. The per-unit canopy biomass effect of loosestrife on reducing colonization will be greater than that of cattail.
4. Reduced colonizer success due to increasing canopy biomass will be more pronounced with added nitrogen (due to threshold effects).
5. At equivalent levels of light availability loosestrife will limit colonizer success more than cattail.
6. Reduced colonizer success due to decreasing light availability will be more pronounced with added nitrogen (a result of threshold effects).

Materials and methods

NATURAL HISTORY OF OUR STUDY SYSTEM

Broad-leaved cattail is highly competitive throughout its native range, commonly forming monocultures or near-monocultures due to its vigorous clonal spread and high productivity (Grace & Harrison 1986). Despite cattail's competitive dominance, loosestrife has invaded millions of hectares of wetlands previously dominated by cattail. Its rate of spread from 1940 to 1980 averaged $1157 \text{ km}^2 \text{ year}^{-1}$ (Thompson, Stuckey & Thompson 1987), and its current distribution includes at least 45 states in the continental US, of which it is now considered noxious in 23 (The Biota of North America Program, <http://www.bonap.org>, accessed 17 June 2010). Empirical data show clearly that loosestrife displaces cattail and that it does so regardless of initial densities (Mal, Lovett-Doust & Lovett-Doust 1997; Weihe & Neely 1997). Furthermore, because broad-leaved cattail is the most common associate of loosestrife in North American wetlands (Thompson, Stuckey & Thompson 1987), past and future population spread by loosestrife puts cattail at risk of large-scale population declines. Therefore the selection of these two species for a study on relative colonizer suppression by community dominants is relevant ecologically and long overdue from a conservation perspective.

EXPERIMENTAL DESIGN

We grew loosestrife and cattail monocultures from locally grown seed ($c. 40\,000 \text{ seeds m}^{-2}$) in an evenly spaced array of wetland mesocosms (1000-L polyethylene livestock watering tanks, 2.1 m^2 surface area) starting in June of 2000 (Fig. 1). Mesocosms were filled with 30 cm of well-mixed nutrient-poor wetland soil, and water levels were kept at 5 cm above the soil surface during the growing season. Soil nitrogen in the mesocosms was manipulated as either low or high (0 or 16 g N m^{-2}) via a yearly application of urea fertilizer. Potassium and phosphorus were added yearly (8 g m^{-2} each, added as muriate of potash and triple-super phosphate, respectively) to ensure nitrogen was the limiting nutrient. Treatment combinations for two separate longer term experiments were allocated randomly within each of six experimental blocks (thus our design was unbalanced; see below).

We manipulated insect herbivory beginning in spring 2001 by introducing a leaf-feeding beetle (*Galerucella californiensis* L.) to $\frac{2}{3}$ of the mesocosms and by spraying the remaining mesocosms with

a broad-spectrum insecticide (S-fenvalerate, trade name AsanaXL) weekly during the growing season. Herbivory and all interactions with herbivory were unrelated to colonizer presence (PROC CATMOD, SAS 8.0; all $P > 0.25$). Likewise, herbivory and its interactions were unrelated to total colonizer biomass, richness and diversity (PROC GLM, all $P > 0.25$). This was expected at the time of our experiment because *G. californiensis* generally requires 4–6 years or more to decrease loosestrife abundances (Lindgren 2003; Grevstad 2006). We harvested colonizers (see below) in the spring of the year following herbivore introduction, before substantial herbivore damage took place. Therefore, all subsequent analyses were conducted by pooling herbivory treatments (Sokal & Rohlf 1995), yielding 30 high-nitrogen and 30 low-nitrogen cattail monocultures and 24 high-nitrogen and 24 low-nitrogen loosestrife monocultures.

DATA COLLECTION

In late May 2001 we measured light availability at the soil surface (diffuse non-interceptance, DIFN) in 105 of the 108 mesocosms using an LAI-2000 leaf canopy analyzer (Li-Cor, Lincoln, NE, USA). Three loosestrife mesocosms were inadvertently skipped (one high-nitrogen and two low-nitrogen). Diffuse non-interceptance at the soil surface accounts for cumulative light capture throughout an herbaceous canopy and is reported as the fraction of sky visible beneath the canopy (thus it is unitless). This measure correlates strongly with light availability (Welles & Norman 1991), and hereafter we refer to DIFN simply as light availability.

We estimated above-ground canopy biomass (g m^{-2}) for loosestrife and cattail monocultures in early August 2001 using allometric relationships derived from additional mesocosms in the array (initiated at the same time and subjected to identical manipulations). Height measurements from 2001 predicted per-stem biomass well for both loosestrife ($R^2 = 0.92$; $F_{1,79} = 859.3$; $P < 0.001$) and cattail ($R^2 = 0.92$; $F_{1,26} = 307.0$; $P < 0.001$).

Colonizing species (e.g. all non-loosestrife seedlings from loosestrife monocultures) were identified and harvested during June 2002, and their above-ground biomass was dried and weighed. This was the first time colonizers had been harvested from the mesocosms, thus our sample assesses all colonization events over a 24-month period. Colonizers either originated from the seed bank within a given mesocosm or from the surrounding vegetation (a moderately diverse sedge meadow). We used per-species or per-morphospecies biomass to calculate Shannon–Wiener diversity (Pielou 1974).

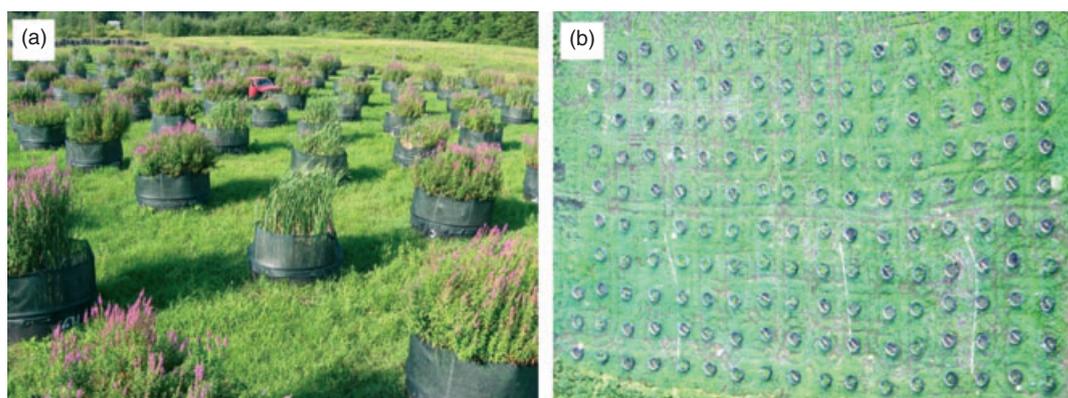


Fig. 1. Experimental layout of mesocosm array, showing (a) ground-level and (b) aerial views. The array consists of 163 mesocosms, 105 of which were used in this experiment. Each 1000-L mesocosm has a surface area of 2.1 m^2 . The area shown in (b) is roughly $85 \times 60 \text{ m}$.

STATISTICAL ANALYSES

We assessed colonization success in a two-stage process using SAS version 8.0 (SAS Institute, Inc., Cary, NC, USA). First we tested the likelihood of a mesocosm being colonized, either by any species or by species of a particular growth form (graminoid or forb), using logistic regression on all 105 mesocosms. For the 76 mesocosms with at least one colonizer we then evaluated how colonizer biomass, species richness and Shannon–Wiener diversity responded to our treatments using general linear models. We did the same analysis for graminoids only and forbs only (in 69 or 47 colonized mesocosms, respectively). Colonizer biomass and species richness were natural-log-transformed, diversity did not require transformation, and residuals for all models were approximately normally distributed.

For each of these measures of colonization success, we used an information-theoretic approach with model averaging to assess the importance of canopy species identity (SPECIES), nitrogen fertilization (FERT), canopy biomass (CANMASS), light availability (LIGHT) and relevant interaction terms. Because SPECIES and FERT were directly manipulated, these terms featured most prominently in our candidate set of 26 models (see Table S1 in Supporting Information). Since LIGHT and CANMASS should be negatively correlated none of our models included both terms, although they were equally represented across the candidate set. We maintained intra-model hierarchical structure so if an interaction term was included both component main effects were as well. CANMASS was natural-log-transformed, LIGHT was arcsine-square-root-transformed and both variables were centred on zero by subtracting the mean.

For each response, we calculated the bias-corrected AIC (AIC_C) and Δ_i for all 26 candidate models, where Δ_i is the difference between AIC_C for model i and the minimum AIC_C (Burnham & Anderson 1998). A smaller AIC_C is better, thus a large Δ_i indicates poor model fit. To minimize bias in our model-averaged parameter estimates, we selected a reduced set of best-fit models (Burnham & Anderson 1998), using only those with $\Delta_i < 3.0$. More conservative approaches ($\Delta_i < 6$ or < 10) did not change our findings (data not shown). We compared models from the reduced candidate set using their Akaike weights (w_i), which are calculated from Δ_i and which estimate the relative likelihood of each model. For any set of models, $\Sigma w_i = 1.0$.

To test our predictions, we assessed individual parameters from these best-fit models using importance weights and model averaging. The importance weight (IW) for a parameter is analogous to the Akaike weight for a model and is calculated by summing the w_i from all models that include it; parameters occurring in every model thus have $IW = 1.0$. Model averaging yields a composite model with weighted-average parameter estimates where the weights are equal to a model's w_i . Variables that did not occur in a given model were assigned parameter estimates of zero. Because some variables are present in only a few models from the original set (Table S1), this method could improperly down-weight a strongly supported effect if the reduced candidate set includes more models than could contain a given parameter. In our analyses this happened twice [cf. the SPECIES \times CANMASS interaction for colonization by forbs (Tables 1 and S3) and the SPECIES \times LIGHT interaction for colonizer diversity (Tables 3 and S4)]. In both cases, we re-normalized Akaike weights so $\Sigma w_i = 1.0$ across the first three or four models, respectively (Burnham & Anderson 1998). We report 95% confidence intervals (CI_{95} ; symmetric around parameter estimates) calculated using Burnham & Anderson's (1998) unconditional variance. This accounts for uncertainty around single-model parameter estimates in

Table 1. Tests of individual parameters for predicting the log odds (logit) that a mesocosm is colonized by any colonizer species or by any graminoid or forb, based on the best-fitting models (with $\Delta_i < 3$)

Parameter	IW	Est.	CI_{95}	OR
Colonization by all species combined				
SPECIES	1.00	-1.31	(-2.01, -0.61)	0.27
FERT	1.00	-0.66	(-1.26, -0.06)	0.52
CANMASS	1.00	-3.23	(-5.98, -0.48)	0.04
FERT \times CANMASS	0.53	-1.26	(-4.32, 1.81)	0.28
SPECIES \times FERT	0.23	-0.01	(-0.18, 0.16)	0.99
SPECIES \times CANMASS	0.09	-0.03	(-0.35, 0.29)	0.97
Colonization by graminoids				
SPECIES	1.00	-1.44	(-2.15, -0.72)	0.24
FERT	1.00	-0.80	(-1.40, -0.20)	0.45
CANMASS	0.67	-1.23	(-3.89, 1.43)	0.29
FERT \times CANMASS	0.52	-1.38	(-4.59, 1.83)	0.25
LIGHT	0.33	0.81	(-1.62, 3.25)	2.25
SPECIES \times FERT	0.23	0.03	(-0.19, 0.26)	1.03
Colonization by forbs				
SPECIES	1.00	-0.48	(-0.95, -0.02)	0.62
CANMASS	1.00	-3.31	(-5.76, -0.85)	0.04
SPECIES \times CANMASS	0.89	-2.51	(-4.95, -0.08)	0.08
FERT	0.53	-0.19	(-0.67, 0.29)	0.83
SPECIES \times FERT	0.15	-0.02	(-0.14, 0.09)	0.98

Importance weights (IW), model-averaged parameter estimates, 95% confidence intervals (CI_{95}) and odds ratios (OR) are given for each parameter. Parameter estimates are the natural log of the odds ratio. The odds ratio for a given parameter thus = $\exp(\text{Est.})$ and represents the factor by which a one-unit change in that parameter either increases ($OR > 1$) or decreases ($OR < 1$) the odds of colonization. For binary parameters (SPECIES and FERT), a negative OR represents decreasing odds of colonization in loosestrife versus cattail mesocosms and in fertilized versus non-fertilized mesocosms. For CANMASS, units are g m^{-2} (natural-log-transformed and centred around zero by subtracting 7.50). See Figs 2 and S2 for interpretation of interactions. Significant parameters (CI_{95} not overlapping zero) are noted in bold.

addition to model-selection uncertainty. Unless otherwise stated below we report untransformed means ± 1 SE.

Results

The assemblage of colonizers was a diverse group of common, mostly native ($> 75\%$) wetland and sedge meadow species (Table S2). Of the 29 morphospecies, 24 were identifiable to species or genus and two to family. The three unidentifiable forbs made up only 0.3% of all colonizer biomass. Richness and colonizer biomass ranged from 0 to 10 species and 0–99 g dry wt per mesocosm, respectively. Thirteen species colonized mesocosms of both canopy species, fifteen colonized only cattail mesocosms and one unidentified forb colonized only loosestrife mesocosms (Table S2).

Colonizers were grouped as graminoids (12 species), herbaceous forbs (14 species) or woody species (*Acer*, *Salix* and *Ulmus* spp.). Graminoids were both the most frequently occurring and the most abundant, based on biomass (Table S2). *Sagittaria latifolia* Willd. was by far the most frequent forb. We analysed the forb response both with and without

S. latifolia to guard against incorrectly interpreting single-species patterns as the full group response. Our results did not vary, so we present only analyses with *S. latifolia* included in the data set.

Loosestrife and cattail mesocosms reduced understorey light availability to nearly identical levels (t -test: $t_{103} = 0.07$, $P = 0.95$; proportion open canopy under loosestrife: 0.16 ± 0.02 vs. cattail: 0.16 ± 0.02), regardless of fertilizer addition (SPECIES \times FERT interaction from two-factor ANOVA: $F_{1,101} = 0.30$, $P = 0.59$). Canopy biomass was similar in loosestrife and cattail mesocosms (1804 ± 55 and 1902 ± 65 g m⁻², respectively), although fertilization did cause a significant increase in cattail biomass only (SPECIES \times FERT interaction: $F_{1,101} = 6.52$, $P = 0.01$; cattail biomass at low N: 1679 ± 88 g m⁻² and at high N: 2125 ± 78 g m⁻²; loosestrife biomass at low N: 1793 ± 77 g m⁻² and at high N: 1815 ± 78 g m⁻²). Canopy biomass and light availability were only weakly correlated for both cattail ($R^2 = 0.06$, $P = 0.06$) and loosestrife ($R^2 = 0.03$, $P = 0.24$).

Below, we present data addressing our six predictions (P1–6), first for all colonizing species and then for graminoids and forbs. Our inferences are primarily based on model-averaged parameter estimates from the reduced set of candidate models (Tables 1 and 3) and on whether the associated CI₉₅ exclude zero (Stephens *et al.* 2005); we refer to these cases as significant. In the single case where only the 90% confidence interval (CI₉₀) of an effect excludes zero we refer to it as marginally significant. As Supporting Information we also present the best-fit models and accompanying model-fit statistics on which all parameter estimates are based (Tables S3–S5).

P1: COLONIZER SUCCESS WILL BE POORER UNDER CANOPIES OF PURPLE LOOSESTRIFE THAN UNDER BROAD-LEAVED CATTAIL

This prediction was well supported. More cattail mesocosms were colonized than loosestrife mesocosms (86.7% vs. 53.3%; Table 1). Total colonizer biomass was twice as high under cattail versus loosestrife canopies (Table 2), although model-averaged parameter estimates suggest canopy species identity was not a good predictor of colonizer biomass (Table 3). Colonizer communities in cattail mesocosms were also significantly more species-rich and diverse than those in loosestrife mesocosms (Tables 2 and 3).

Graminoids and forbs colonized more cattail than loosestrife mesocosms as well (graminoids: 85.0% vs. 40.0% and forbs: 51.7% vs. 35.6%; Table 1). Graminoids had marginally higher biomass under cattail canopies, and they were significantly more species-rich and diverse in cattail than loosestrife mesocosms (Tables 2 and 3). Contrary to our expectation, forb biomass was over three times higher under loosestrife canopies than under cattail (Tables 2 and 3). Forb richness and diversity were similar under cattail and loosestrife canopies, primarily because no statistical model could explain the relatively limited variation in either measure (all $R^2 \leq 0.06$ and all parameter CI₉₀ included zero; models not shown; see Table 2 for averages).

Table 2. Mean colonizer biomass, richness and Shannon–Wiener diversity, grouped by canopy species identity and fertilization treatments

	All colonizers ($n = 76$)	Graminoids ($n = 69$)	Forbs ($n = 47$)
Colonizer biomass (g)			
Loosestrife	10.9 (2.2)	9.5 (2.2)	4.2 (1.4)
Cattail	21.9 (3.2)	21.6 (3.2)	1.2 (0.7)
High N	18.1 (3.6)	18.2 (3.3)	1.9 (1.2)
Low N	18.7 (3.1)	18.7 (4.0)	2.4 (0.8)
Colonizer richness			
Loosestrife	2.5 (0.4)	1.6 (0.2)	1.5 (0.3)
Cattail	3.8 (0.3)	2.8 (0.2)	1.4 (0.1)
High N	3.1 (0.4)	2.4 (0.3)	1.2 (0.1)
Low N	3.6 (0.3)	2.5 (0.2)	1.6 (0.2)
Colonizer S–W diversity			
Loosestrife	0.43 (0.10)	0.26 (0.09)	0.18 (0.09)
Cattail	0.67 (0.05)	0.58 (0.06)	0.11 (0.04)
High N	0.52 (0.08)	0.47 (0.08)	0.06 (0.04)
Low N	0.65 (0.07)	0.52 (0.07)	0.18 (0.33)

For each response, we show raw averages (with SE in parentheses) across colonized mesocosms only.

P2: INCREASING NITROGEN FERTILIZATION WILL LOWER COLONIZATION OVERALL, BUT IT WILL DO SO TO A GREATER EXTENT UNDER LOOSESTRIFE THAN UNDER CATTAIL

This did not occur. Although fertilization decreased the percentage of mesocosms that were colonized from 84.6 to 60.4% (Table 1), it had no effect on total colonizer biomass, richness or diversity (Tables 2 and 3). Fertilization also did not cause a greater decline in colonization under loosestrife canopies relative to cattail (all SPECIES \times FERT IW ≤ 0.23 and all CI₉₀ included zero; Tables 1 and 3).

Fertilization reduced how many mesocosms were colonized by graminoids (78.8% vs. 52.8%) and forbs (53.8% vs. 35.8%) by similar proportions, although the forb response was not statistically significant (Table 1). Fertilization did not affect the biomass, richness or diversity of either graminoids or forbs (Tables 2 and 3).

P3: THE PER-UNIT CANOPY BIOMASS EFFECT OF LOOSESTRIFE ON REDUCING COLONIZATION WILL BE GREATER THAN THAT OF CATTAIL

This did not occur except for forb colonization. For all colonizers combined, mesocosms with more canopy biomass were less likely to be colonized, regardless of canopy species identity (non-significant SPECIES \times CANMASS interaction; Table 1). In support of our prediction, however, loosestrife reduced the likelihood of forb colonization more than cattail per-unit biomass such that most high-biomass loosestrife mesocosms lacked forb colonizers (significant SPECIES \times CANMASS interaction; Table 1; Fig. 2). Based on the model-averaged predicted response, the odds of forb colonization drop off nearly 10 times faster under loosestrife than

Table 3. Tests of individual parameters for predicting colonizer biomass, richness and diversity, based on the best-fitting models (with $\Delta_i < 3$)

Parameter	Biomass (g)		Species richness		S-W diversity	
	IW	CI ₉₅	IW	CI ₉₅	IW	CI ₉₅
All colonizers						
SPECIES	0.87	(-1.03, 0.12)	1.00	(-0.50, -0.13)	1.00	(-0.42, -0.02)
LIGHT	1.00	(1.00, 4.03)	1.00	(0.67, 1.93)	1.00	(0.40, 1.75)
FERT	0.37	(-0.42, 0.23)	0.81	(-0.34, 0.07)	0.68	(-0.32, 0.11)
FERT × LIGHT	0.19	(-0.96, 1.69)				
SPECIES × LIGHT	0.15	(-0.76, 0.51)	0.82	(-1.17, 0.42)	0.72	(-1.79, 0.34)
SPECIES × FERT			0.14	(-0.06, 0.06)	0.13	(-0.09, 0.06)
Graminoids						
SPECIES	<i>0.91</i>	<i>(-1.24, 0.11)</i>	1.00	(-0.49, -0.16)	1.00	(-0.49, -0.09)
LIGHT	0.79	(-0.49, 4.34)	1.00	(0.75, 1.72)	1.00	(0.56, 1.77)
FERT	0.17	(-0.12, 0.10)	0.41	(-0.16, 0.08)	0.40	(-0.19, 0.10)
SPECIES × LIGHT	0.37	(-3.51, 1.79)	1.00	(-1.95, -0.34)	1.00	(-2.35, -0.34)
CANMASS	0.21	(-1.28, 0.69)				
SPECIES × CANMASS	0.07	(-0.34, 0.53)				
Forbs						
SPECIES	1.00	(0.27, 1.20)				
LIGHT	0.78	(-1.04, 1.58)				
FERT	0.63	(-0.72, 0.27)				
FERT × LIGHT	0.31	(-1.45, 2.85)				
SPECIES × LIGHT	0.23	(-0.97, 1.72)				
SPECIES × FERT	0.06	(-0.07, 0.06)				

Importance weights (IW) and 95% confidence intervals (CI₉₅; symmetric around the model-averaged estimate) are given for each parameter. Significant and marginally significant parameters (CI₉₅ or CI₉₀ not overlapping zero) are noted in bold or italics, respectively. LIGHT is the proportion of open canopy (arcsine-square-root-transformed and centred around zero by subtracting 0.37). Colonizers tended to be more successful in cattail mesocosms, non-fertilized mesocosms and mesocosms with increased light availability or decreasing canopy biomass. The only exception to these patterns was higher forb biomass in loosestrife than cattail mesocosms.

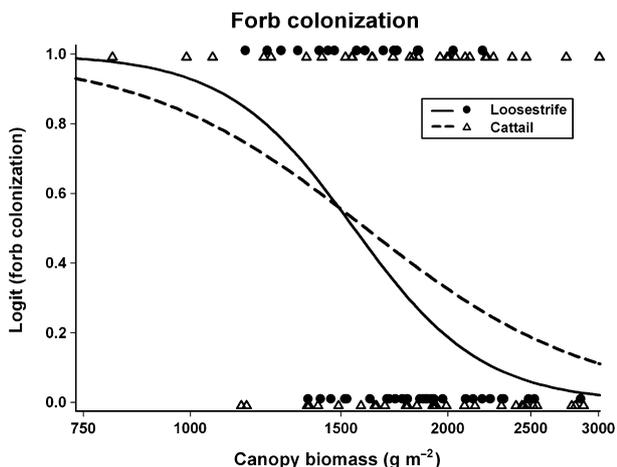


Fig. 2. The probability of forb colonization declines faster in response to increasing canopy biomass under loosestrife versus cattail canopies (significant SPECIES × CANMASS interaction). Curves show model-averaged predictions, and symbols indicate mesocosms with or without forb colonizers (1.0 or 0.0 on the y-axis, respectively). Symbols are offset in the y-direction to facilitate interpretation. Odds ratios are calculated as $\exp(b_1)$, where b_1 is the parameter estimate for CANMASS. The odds ratio is interpreted as the relative change in the odds of an event occurring (here, forb colonization) with each 1-unit increase in the independent variable. The odds ratio for loosestrife = $\exp(-5.82) = 0.0030$ and for cattail = $\exp(-3.31) = 0.037$, a nearly tenfold difference. Note that canopy biomass is on a log_e scale.

under cattail given the same increase in canopy biomass (odds ratio for loosestrife = 0.0030 and for cattail = 0.037; Fig. 2). No other measure of colonizer success was lower in loosestrife than cattail mesocosms per-unit canopy biomass. This may be partly due to variation in canopy biomass explaining very little variation in colonizer biomass, richness or diversity (Fig. S1).

P4: REDUCED COLONIZER SUCCESS DUE TO INCREASING CANOPY BIOMASS WILL BE MORE PRONOUNCED WITH ADDED NITROGEN

We found little support for this prediction. Increases in canopy biomass slightly lowered the likelihood of graminoid colonization in fertilized relative to non-fertilized mesocosms, but the FERT × CANMASS interaction was not statistically significant and was not consistently included in best-fit models (IW = 0.53; Tables 1 and S3; Fig. S2).

P5: AT EQUIVALENT LEVELS OF LIGHT AVAILABILITY LOOSESTRIFE WILL LIMIT COLONIZER SUCCESS MORE THAN CATTAIL

This prediction was well supported because increasing light availability caused a significant increase in colonizer richness and diversity in cattail mesocosms only (Fig. 3b,c). Colonizer

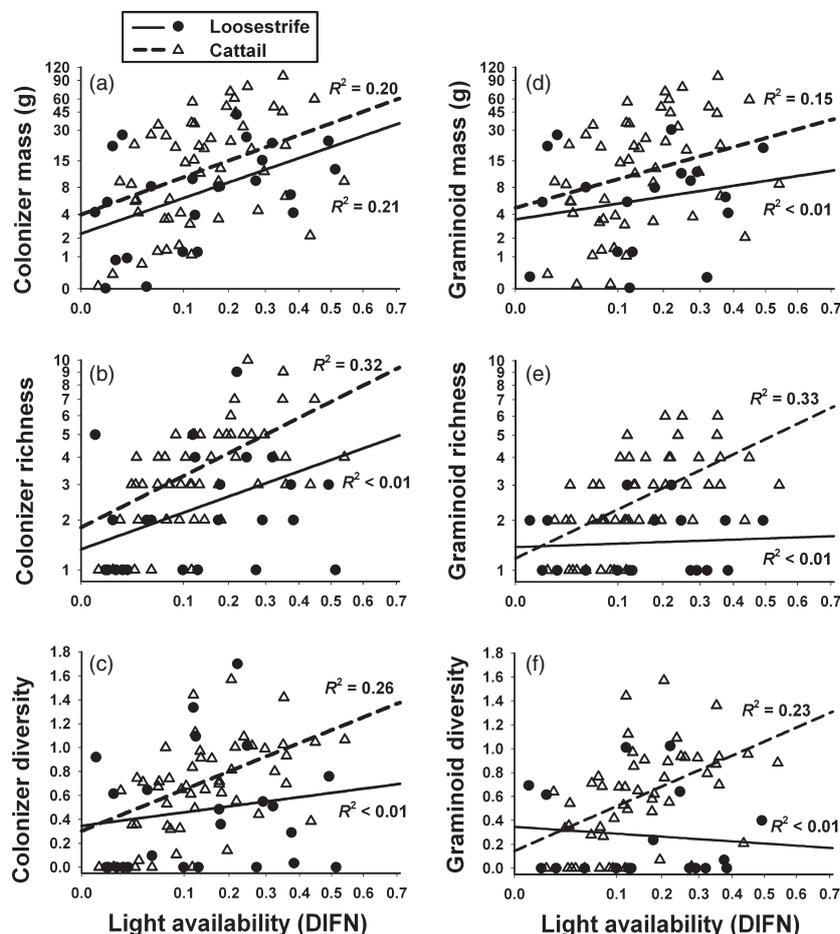


Fig. 3. The change in colonizer biomass, richness and Shannon–Wiener diversity in response to May 2001 light availability, graphed separately for all colonizers (a–c) and for graminoid colonizers only (d–f). Regression lines are model-averaged solutions from Table 3 (including SPECIES \times LIGHT interactions). Note that biomass and richness are on a \log_e scale and light availability is transformed as $\arcsin(\text{DIFN}^{0.5})$, where DIFN is diffuse non-interceptance.

biomass, however, increased with light availability regardless of canopy species (Fig. 3a). Differences in the competitive effects of loosestrife and cattail at equivalent light availability (i.e. when they cast the same amount of shade) were driven primarily by the graminoid response. Graminoid richness and diversity increased with light under cattail but not under loosestrife when light availability was the same beneath canopies of each species (significant SPECIES \times LIGHT interaction; Table 3; Fig. 3e,f).

P6: REDUCED COLONIZER SUCCESS DUE TO DECREASING LIGHT AVAILABILITY WILL BE MORE PRONOUNCED WITH ADDED NITROGEN

This prediction was weakly supported for forb biomass only. Light availability explained variation in forb biomass in fertilized ($R^2 = 0.16$) but not unfertilized mesocosms ($R^2 < 0.01$). However, the FERT \times LIGHT interaction was not statistically supported for any measure of colonizer success (all CI_{90} included zero; Tables 1 and 3).

Discussion

Purple loosestrife suppressed colonization much more than broad-leaved cattail did, consistent with our predictions and based on nearly every measure of colonizer success. Moreover,

uncommon colonizers were only found in cattail mesocosms. With only one exception (colonization by forbs), loosestrife and cattail had similar competitive effects per unit biomass. This was not the case when loosestrife and cattail intercepted light to the same extent. As light availability increased (i.e. as canopy species cast less shade), colonizer richness and diversity increased under cattail but not under loosestrife (Fig. 3). Furthermore, responses by forbs and graminoids differed fundamentally; forbs had higher biomass under loosestrife and graminoids had higher biomass under cattail. Overall, our study is the first to demonstrate experimentally that an invasive suppresses colonization more than a dominant native species. We are also the first to show that direct measures of resource availability can provide a more informative standardization than does biomass when assessing competitive effects of community dominants.

ASSESSING COMPETITIVE EFFECTS BY MEASURING RESOURCE AVAILABILITY

We attempted to standardize competitive effects by canopy biomass, but it explained surprisingly little variation in colonizer success. Although competitive effects have rarely been quantified, the usual method is to correlate the response of a target species or community with competitor biomass; stronger competitors therefore have steeper slopes (Goldberg & Werner

1983). Strong negative relationships between competitor biomass and target species performance have been found (e.g. Freckleton & Watkinson 2001; Violle *et al.* 2009); however, competitor biomass often has limited explanatory power, particularly in highly productive systems (Grace 1999; Hager 2004). This suggests that an alternative method for assessing competitive effects may be needed, especially for highly productive community dominants. Measuring competitive effects on a per-capita basis is one possibility, but not for the many herbaceous dominants (including loosestrife and cattail) that reproduce clonally. We believe ours is the first study to compare species' competitive effects standardized based on a direct measure of resource availability (i.e. light) rather than on plant-based measures that should correlate with resource uptake. Using this approach, we found that increasing light availability led to higher graminoid richness and diversity beneath cattail but not loosestrife canopies. Therefore, something other than light limitation at the soil surface must explain low graminoid richness and diversity under loosestrife canopies.

Intense below-ground competition may be the answer. In our mesocosms, loosestrife roots are densely packed high in the soil profile whereas most cattail root biomass is in the form of rhizomes that are located much deeper (Fig. 4). A dense surface layer of roots may be inimical to colonizers establishing from seed, making colonization and early growth more likely in cattail monocultures. Strong competition for below-ground resources could also explain why light availability was a relatively unimportant predictor for colonizer success under loosestrife. Evaluating competitive effects standardized by *below-ground* biomass would be insightful in this regard, but unfortunately we did not collect these data at the time when colonizers were harvested. Overall, our findings show that standardizing competitive effects by light availability permits a comparison of competitor impacts when that resource is equally limiting, which can in turn help identify putative mechanisms of competitive exclusion.

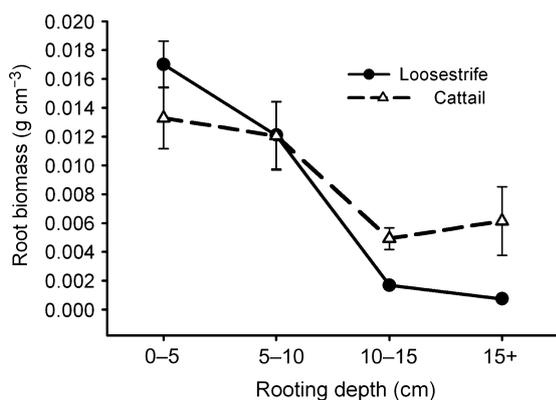


Fig. 4. Contrasting root distributions in cattail and loosestrife monocultures. Roots were collected in August 2008 (2 cores per mesocosm; 10.2 cm diameter, 26–33.5 cm deep). Data is dry wt biomass cm⁻³ soil (± 1 SE, $n = 12$ mesocosms for loosestrife and 8 for cattail). Error bars for loosestrife beyond 10 cm depth are masked by the data points.

IMPLICATIONS FOR NATIVE PLANT COMMUNITIES

Colonizer suppression was greater in loosestrife than cattail monocultures, and uncommon species were essentially absent beneath loosestrife. This suggests that widespread displacement of cattail by loosestrife could result in species-poor communities that lack rare species (see also Farnsworth 2004). Further, graminoid suppression by loosestrife suggests that loosestrife invasions may affect graminoid relative abundances, impacting wetland systems in unpredictable ways. These dynamics may be delayed for many years following invasion if native species are excluded slowly and colonizer re-establishment is consequently suppressed. Such a lag could divorce the relatively moderate impacts of an initial invasion from the long-term consequences for the native community.

Unexpectedly, and in contrast to the graminoid response, forbs produced three times more biomass in loosestrife than cattail mesocosms (with no parallel increase in forb diversity). This finding is consistent with strong below-ground competition by loosestrife because our common graminoid colonizers are relatively shallow-rooted and our common forb colonizers are deep-rooted. For example, the forb *Sagittaria latifolia* produces corms at depths similar to cattail rhizomes but below most loosestrife root mass (S. M. Hovick, pers. obs.). Others have reported an association between loosestrife and *S. latifolia* (Jean & Bouchard 1993; Keller 2000; Hager & Vinebrooke 2004), but an increased likelihood of co-occurrence due to contrasting root depths was not discussed. If this pattern did apply broadly to deep-rooted species, it would help reconcile conflicts regarding loosestrife's impacts on wetland diversity. We admit that until below-ground resources are quantified, this inference is speculative; nevertheless, the pattern is intriguing and warrants further study.

FAIR COMPARISONS USING DOMINANT SPECIES PAIRS

A fair assessment of invasive species' impacts should compare invaders with native dominant species. Using this approach, we found loosestrife to be a stronger competitor with more detrimental community-level impacts than broad-leaved cattail. Invasive competitiveness is commonly compared with that of native species, but usually the native is a weak competitor (Vilà & Weiner 2004; Vilà, Williamson & Lonsdale 2004) and thus conclusions from these studies are somewhat tenuous. We recognize the limitations inherent in a comparison involving only one dominant species pair. However, because loosestrife is displacing cattail over vast regions of North America our comparison directly addresses an ecologically important dynamic. Our experimental approach could be conducted with additional pairs of community dominants from a range of systems, and meta-analysis could then be used to assess whether invasives truly have greater impacts than dominant native species.

FERTILIZATION SUPPRESSES COLONIZERS VIA CANOPY SPECIES PRODUCTIVITY

As expected, nitrogen fertilization decreased colonization. However, this effect was much less important than increases in

canopy biomass or decreases in light availability, strongly suggesting that the impact of nutrient addition was mediated via increased productivity in the canopy species (Carson & Pickett 1990). We found only weak support for fertilization-based threshold effects, suggesting that threshold levels of biomass required to suppress graminoid colonization may occur only with very high biomass (see Fig. S2). We found no support for disproportionate effects by loosestrife relative to cattail in fertilized mesocosms (no SPECIES \times FERT interaction).

RECONCILING CONFLICT REGARDING LOOSESTRIFE'S IMPACT ON DIVERSITY

Although the negative repercussions of loosestrife invasions on wetland communities are well documented (Gabor, Haagsma & Murkin 1996; Weiher *et al.* 1996), some have argued that loosestrife's impacts on diversity are exaggerated (Treberg & Husband 1999; Hager & Vinebrooke 2004). We found strong support for loosestrife's competitive superiority, even when compared to the highly competitive broad-leaved cattail. To our knowledge the only other study comparing the impacts of loosestrife and cattail on community diversity documented equivalent effects on species richness from surveys in Ontario wetlands (Houlahan & Findlay 2004). In that study, dominant species abundance was estimated at the scale of an entire wetland, but since most competitive interactions between plants occur at the neighbourhood scale, species richness at larger scales may be a poor metric for assessing these impacts. Although we agree with Houlahan & Findlay (2004) that any dominant species can suppress plant community diversity, our data strongly suggest that loosestrife does so to a greater extent than cattail.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. The full set of models used to calculate AIC_C for all response variables.

Table S2. Frequency of occurrence and mean biomass of colonizers collected in June 2002.

Table S3. Best models ($\Delta_i < 3$) for predicting the probability that a mesocosm is colonized, either for all colonizers combined or for graminoids or forbs.

Table S4. Best models and associated parameters for predicting biomass, richness and diversity of all colonizers.

Table S5. Best models and associated parameters for predicting biomass of graminoids and broad-leaved forbs.

Figure S1. Colonizer biomass, richness and diversity in relation to canopy species identity and canopy biomass.

Figure S2. The probability of graminoid colonization in response to increasing canopy biomass differs slightly in high N and low N mesocosms, although the FERT \times CANMASS interaction is non-significant.

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