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Flood tolerance in wetland angiosperms: a comparison of invasive and noninvasive species

Suzanne M. Kercher, Joy B. Zedler*

Department of Botany, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, WI 53706, USA

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Abstract

We assessed the biomass production, biomass allocation patterns, height growth, and root airspace of seventeen wetland plant taxa, including two potentially invasive species, grown under high nutrient conditions and subjected to four hydrologic regimes: constant drawdown, cyclic flooding and drawdown, cyclic flooding and drought, and constant flooding for the duration of the experiment (∼10 weeks). We found that: (1) the potentially invasive reed canary grass (*Phalaris arundinacea*) and broadleaf cattail (*Typha latifolia*) responded to treatments similarly; both outgrew the other perennial species in all four hydrologic regimes; (2) *Phalaris* had the highest levels of root airspace of all the taxa; (3) the grasses and graminoids nearly always tolerated flooding better than the broadleaf forbs, perhaps in part due to greater quantities of root airspace; and (4) the species that were most sensitive to flooding are typically found in drier, groundwater-fed, and more nutrient-poor environments. We hypothesize that *Phalaris* and *Typha*, which are both tall and productive, should be competitive dominants under a variety of hydrologic conditions, at least where nutrients are abundant, as in urban and agricultural landscapes. Eight of the noninvasive taxa tolerated flooding but produced less biomass and/or were shorter or shorter-lived than *Phalaris* and *Typha*. Among the five taxa that were most sensitive to flooding were slow-growing habitat specialists; such species will likely experience declines in areas that become impounded or experience greater volumes of runoff.
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Keywords: Invasive species; *Phalaris arundinacea*; *Typha latifolia*; Urban runoff; Wetland plants

* Corresponding author. Tel.: +1 608 262 8629; fax: +1 608 262 7509.
E-mail address: jbzedler@wisc.edu (J.B. Zedler).

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1. Introduction

Hydrologic conditions, especially flooding regimes, are known to be a strong if not primary influence on wetland plant community composition and processes (Mitsch and Gosselink, 1993; Keddy, 2000). When affected by urban development, natural hydrologic regimes typically have increased frequency and severity of flooding (Watson et al., 1981; Pitt, 1996; Detenbeck et al., 1999), lowered water tables and reduced groundwater recharge (Brinson, 1993) compared to previous, more natural conditions. Associated shifts in the vegetation of temperate freshwater wetlands include a loss of biodiversity, decreased floristic quality and an expansion of invasive plant species (Galatowitsch et al., 2000; Brinson and Malvarez, 2002; Choi and Bury, 2003; Kercher et al., 2004).

"Invasive plants" are species or strains that rapidly increase their spatial distribution by expanding into existing plant communities. Based on a survey of the literature, Richardson et al. (2000) define invasive plants as plants "that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants (approximate scales: >100 m, <50 years for taxa spreading by seeds and other propagules; >6 m/3 years for taxa spreading by roots, rhizomes, stolons, or creeping stems), and thus have the potential to spread over a considerable area" (p. 98). Although invasive plants are often exotic, they are sometimes native (e.g., *Typha domingensis* in the Florida Everglades; Wu et al., 1997) or hybrids between native and exotic strains (e.g., *Typha* × *glauca*; Galatowitsch et al., 1999). In North America, two plant species that are invasive by this definition are reed canary grass (*Phalaris arundinacea*), an erect, cool season perennial grass that occurs in 43 of the United States plus Canada, and broadleaf cattail (*Typha latifolia*), an erect perennial semi-aquatic graminoid that is ubiquitous throughout North America and occurs in all 50 of the United States plus Canada and Mexico (Wisconsin State Herbarium, 2003; USDA and NRCS, 2003). Although both are native to North America, *Phalaris* and *Typha* are capable of spreading large distances via seed and rhizome fragments and, once established in a wetland, can undergo rapid clonal spread and form dense monotypic stands with few coexisting species (Grace and Wetzel, 1981; Barnes, 1999; Veltman, 2002; Kercher et al., 2004).

Although the process of conversion to a monotype has not been well-studied, greater tolerance of flooding may be one factor that favors invasive plants like *Phalaris* and *Typha* in stormwater-impacted wetlands (Zedler and Kercher, 2004). Several researchers have experimentally investigated the flooding responses of herbaceous hydrophytes (e.g., Lieffers and Shay, 1981; Rubio et al., 1995; Ewing, 1996; Lentz and Dunson, 1998; Hunter et al., 2000; Clarke and Baldwin, 2002; Bonilla-Warford and Zedler, 2002), but fewer studies have compared the flooding responses of invasive and noninvasive wetland species (Newman et al., 1996; Lempe et al., 2001; Vandersande et al., 2001; Miller and Zedler, 2003). We grew seventeen wetland plant taxa, including the two invasive species *P. arundinacea* and *T. latifolia*, and subjected them to four hydrologic regimes within experimental pots. Our goals were: (1) to assess the flood tolerance (defined here as the ability to produce biomass under flooded conditions relative to unflooded conditions) of the noninvasive and invasive taxa; (2) to rank taxa in each experimental environment relative to other taxa on the basis of biomass production and height growth, two variables that affect a

taxon's ability to dominate (Grime, 1979); and (3) to assess whether the differential flood tolerance of taxa relates to root airspace, growth rates, and/or biomass allocation patterns.

2. Methods

2.1. Experimental setup

We conducted the experiment within a fenced outdoor research facility at the University of Wisconsin-Madison Arboretum (Dane County, Wisconsin, USA; latitude 43.7°, longitude 89.20°) during the summer of 2000. We employed a completely randomized design and varied two factors, taxon and hydrologic treatment. We grew 16 species (Table 1) and two source populations of *Spartina pectinata* under four hydrologic regimes. The 17 taxa were selected from a pool of 29 on the basis of high seed germinability and production of ample seedlings. There were five replicates of each taxon-treatment combination for a total of 340 experimental units. Each unit consisted of a 19-l white plastic bucket with a 3.8-l plastic nursery pot inside. Pots received the following treatments (Fig. 1): (1) watered constantly from the bottom with ∼5 cm of standing water but never flooded, or constant drawdown (hereafter called the "Low" treatment); (2) flooded with 15 cm of water above the soil surface for 4 days and then watered from the bottom for 4 days ("4 High/4 Low"); (3) flooded 15 cm for 4 days and then not watered for 4 days ("4 High/4 Dry"); or (4) constantly flooded with 15 cm of water ("High").

Seeds of the grass, sedge, and forb taxa were collected from wild populations (*P. arundinacea*, *Solidago gigantea*, *S. pectinata*, and *T. latifolia*) in Wisconsin or purchased from native plant nurseries. After a month of cold-moist stratification, seeds were sown in flats in a greenhouse at the University of Wisconsin on April 26–27, 2000. Seedlings were

Table 1
Sixteen species chosen for experimentation. Data are scientific name, plant family, and common name (USDA and NRCS, 2003)

Species	Family	Common name
S. pectinata Bosc ex Link	Poaceae	Prairie cordgrass
P. arundinacea L.	Poaceae	Reed canary grass
T. latifolia L.	Typhaceae	Broadleaf cattail
Asclepias incarnata L.	Apocynaceae	Swamp milkweed
B. ciliatus L.	Poaceae	Fringed brome
C. canadensis (Michx.) Beauv.	Poaceae	Bluejoint grass
C. granularis Muhl. ex Willd.	Cyperaceae	Limestone meadow sedge
C. stricta Lam.	Cyperaceae	Upright sedge
E. maculatum L.	Asteraceae	Spotted joe-pye weed
Glyceria striata (Lam.) A. S. Hitchc.	Poaceae	Fowl mannagrass
O. riddellii (Frank ex Riddell) Rydb.	Asteraceae	Riddell's goldenrod
Symphyotrichum puniceum (L.) A. & D. Löve	Asteraceae	Purplestem aster
Eupatorium perfoliatum L.	Asteraceae	Common boneset
H. grosseserratus Martens	Asteraceae	Sawtooth sunflower
S. gigantea Ait.	Asteraceae	Giant goldenrod
B. cernua L.	Asteraceae	Nodding beggartick

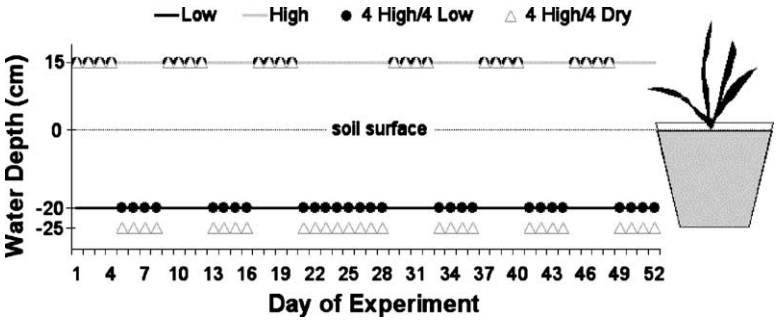

Fig. 1. Depiction of the four experimental hydrologic regimes over time (days). Water depths are relative to the soil surface in the pots.

transplanted to plug trays containing Metro Mix® 360 approximately 2 weeks after germination, kept in a greenhouse with natural light and temperatures that ranged from 24 to 33 °C, and watered daily. On June 28, we filled nursery pots with locally-quarried, screened sand and transferred one plant to each pot. Two Osmocote® Plus controlled release fertilizer tablets (Scotts Europe b.v., Waardenburg, The Netherlands) were added to opposite sides of each pot, halfway between the plant and the side of the pot. Each pot was then placed within its own bucket and watered daily until the experiment began.

On July 9 (day 1), treatments were initiated by filling the white buckets from the bottom with a garden hose until the proper water level was attained. Floods were administered a total of six times: on July 9, July 17 (day 9), July 25 (day 17), August 6 (day 29), August 14 (day 37), and August 22 (day 45). Nearly 10 cm of rain fell in a series of thunderstorms that occurred during the third dry/drawdown period (July 30 through August 5). As a result, this dry/drawdown period was extended until four consecutive days had no rainfall. At the end of every flood cycle, all 340 buckets were emptied, scrubbed to remove algae, and filled with fresh water. Throughout this experiment, the soil in the pots was consistently within 1–2 °C of ambient temperature.

We monitored plants regularly for flowering/fruiting status, presence of adventitious roots, and mortality (defined here as no living tissue above the soil surface). Height of the tallest stem, including the inflorescence when present, was measured initially on July 9 and subsequently on September 8. On August 30 (day 53), the last day of the final eight-day cycle, all pots from the 4 High/4 Low and 4 High/4 Dry treatments were subjected to drawdown conditions (i.e., watered from the bottom with ~5 cm of standing water) until plants were harvested beginning on September 18, 2000 (day 72). High treatment buckets remained flooded until biomass was harvested.

2.2. Biomass collection

Shoot biomass was harvested by cutting plant stems at the soil surface. Root biomass, including rhizomes when present, was washed of sand and debris over a wire mesh screen. At this time, three segments of lateral root measuring <10 cm long were collected from different regions of the same plant and stored in a refrigerator until they were used to

estimate root airspace (see below). Root segments could not be collected from some plants due to a near-complete mortality of roots (e.g., *Carex granularis* in the High treatment). Shoot and root biomass was oven dried for 48 h at 60 °C and weighed to the nearest 0.1 g. The root subsamples were excluded from the root biomass measurements since they weighed less than 0.1 g combined.

2.3. Root airspace

Aerenchyma, or root airspace, was estimated for each plant as the percentage weight increase of root samples following vacuum extraction of air and its replacement by water—i.e., 100 × [(final weight of the root subsample − initial weight)/(initial weight)]. This was similar to the methods used by Byott (1976) and Johnston (1977) to measure leaf mesophyll airspace. Immediately prior to vacuum extraction, each root was patted dry with a tissue and weighed to the nearest 0.001 g. To distinguish among the three root subsamples following vacuum extraction, root tips were color marked with a permanent marker.

The vacuum apparatus employed a 250-mL flask connected to a vacuum pump, which was powered by an AC motor. Approximately 200 mL of water was added to the flask, and the three pieces of root from a single plant were placed in the flask and weighted with a paper clip to keep them submerged. The flask was stoppered and the vacuum applied for exactly two minutes. Thereafter, the roots were again patted dry with a clean tissue and promptly reweighed.

2.4. Statistical analyses

Two-way ANOVAs with taxon and treatment as independent variables were performed in SAS Institute Inc. (1999) using a general linear modeling procedure and the following response variables: shoot, root, and whole-plant biomass, shoot:root biomass ratios, and final plant height. A mixed modeling procedure was used to assess the effects of taxon and treatment on percent root airspace. Following significant F-tests, the LSD procedure was used to separate overall treatment and taxon means, and the 'slice' command was used to test for simple effects—i.e., differences among taxa within each treatment and differences among treatments within each taxon. For pairwise comparisons of taxa within treatments, we used a Bonferroni-corrected alpha of 0.0004; and for comparisons of treatments within taxa, we used alpha = 0.0005.

A ''flood sensitivity value'' was calculated for each taxon as [1 − (mean whole-plant biomass produced in the three flooded treatments)/(mean whole-plant biomass produced in the Low treatment)]. We use the terms ''sensitive'' and ''tolerant'' throughout this paper to denote opposite responses to flooding—sensitive taxa had the lowest biomass production in the flooded treatments relative to the Low treatment, while tolerant taxa had the highest production in the flooded treatments relative to the Low treatment.

Relationships among response variables were assessed using simple linear regressions in S-plus 2000 (Mathsoft Inc., 1988–1999). Alpha = 0.05 for all statistical tests, except as noted above.

3. Results

Of the 340 plants, 38 (11%) died during the experiment (Table 2). No plants died in the Low treatment, while 13, 12, and 13 plants died in the 4 High/4 Low, 4 High/4 Dry, and High treatments, respectively. A total of 140 of the 340, or 41%, of the plants flowered before they were harvested; 73% of the plants in the Low treatment flowered, and all taxa except *Calamagrostis canadensis*, *Carex stricta*, and *T. latifolia* yielded at least one flowering individual during the experiment (Table 3). For most taxa, flooding resulted in higher shoot:root ratios but less biomass accumulation, shorter plants, and a lower percentage of flowering individuals (Tables 2 and 3).

The two-way ANOVAs for shoot biomass, root biomass, whole-plant biomass, shoot:root ratios, and final plant height were significant for taxon and treatment ($P < 0.0001$ for all; Table 4). Taxon × treatment interactions were also highly significant ($P < 0.0001$) in all cases. Taxa that produced the most biomass in the Low treatment were *Bidens cernua*, *T. latifolia*, *P. arundinacea*, and *C. stricta* in decreasing order (Table 5 and Fig. 2). Taxa that produced the least biomass in the Low treatment were *Bromus ciliatus*, *Eupatorium maculatum*, *S. gigantea*, and *Oligoneuron riddellii* in increasing order (Table 5 and Fig. 2). Overall, taxa produced significantly more biomass in the Low treatment than in the flooded treatments. The tallest taxa were *T. latifolia* and *S. pectinata*, which grew to 1.3 m in under 5 months, while the shortest taxa were *B. ciliatus*, *E. maculatum*, and *O. riddellii*, none of which exceeded 0.5 m in height (Tables 3 and 5).

The increased shoot:root biomass ratios for all taxa in the flooded treatments were due to (1) reduced root biomass in the flooded treatments relative to the Low treatment, which was

Table 2
Mortality of 17 taxa subjected to three flooding regimes (presented as the number of plants that died out of five possible) and taxon sensitivities to flooding[a]

Taxon	4 High/4 Low	4 High/4 Dry	High	Sensitivity[a]
B. ciliatus	5	3	5	0.98
H. grosseserratus	4	4	2	0.95
E. maculatum	3	1	0	0.88
O. riddellii	0	1	5	0.81
C. granularis	0	0	0	0.66
S. gigantea	0	0	0	0.61
E. perfoliatum	0	0	0	0.56
A. incarnata	0	0	0	0.55
S. puniceum	0	0	0	0.48
B. cernua	0	3	0	0.40
G. striata	0	0	0	0.38
S. pectinata-Koshkonong	1	0	0	0.38
C. canadensis	0	0	1	0.33
C. stricta	0	0	0	0.23
P. arundinacea	0	0	0	0.19
T. latifolia	0	0	0	0.15
S. pectinata-Sumner	0	0	0	0.09

Taxa are listed from most to least sensitive to flooding.

[a] Sensitivity = 1 − [(mean whole-plant biomass in the three flooded treatments)/(mean whole-plant biomass in the Low treatment)].

Table 3
Summary data for 17 taxa: total number of plants to flower in the Low treatment ($n = 5$) and flooded treatments ($n = 15$), number with adventitious roots in the High treatment ($n = 5$), shoot:root biomass ratios in the Low treatment (+S.E.) and flooded treatments, final plant height in the Low treatment and flooded treatments, and root airspace in the Low and flooded treatments

Taxon	Flowering plants; low	Flowering plants; flooded	Advent. roots; high	Shoot:root; low	Shoot:root flooded	Final height (cm); low	Final height (cm); flooded	Root airspace; low	Root airspace; flooded
B. ciliatus	1	0	0	3.8 ± 1.2	6.5 ± 3.5	20 ± 5	12 ± 1	0.22 ± 0.16	NA
H. grosseserratus	5	1	3	4.7 ± 2.6	16.3 ± 10.5	151 ± 11	44 ± 10	0.23 ± 0.07	NA
E. maculatum	5	7	4	1.8 ± 0.7	9.5 ± 2.6	44 ± 2	27 ± 4	0.05 ± 0.02	0.35 ± 0.08
O. riddellii	0	1	0	1.7 ± 0.1	7.0 ± 2.1	47 ± 2	29 ± 3	0.34 ± 0.12	0.15 ± 0.07
C. granularis	3	0	0	1.9 ± 0.4	4.7 ± 1.0	66 ± 7	36 ± 6	0.82 ± 0.24	0.62 ± 0.18
S. gigantea	2	2	5	2.3 ± 0.3	13.4 ± 3.9	56 ± 7	43 ± 5	0.14 ± 0.04	0.17 ± 0.06
E. perfoliatum	10	10	5	0.5 ± 0.1	1.1 ± 0.3	52 ± 3	41 ± 1	0.29 ± 0.08	0.23 ± 0.03
A. incarnata	5	3	5	1.4 ± 0.3	1.6 ± 0.1	109 ± 4	83 ± 2	0.19 ± 0.03	0.18 ± 0.01
S. puniceum	10	10	5	2.2 ± 0.4	2.9 ± 0.5	87 ± 6	80 ± 4	0.31 ± 0.02	0.38 ± 0.04
B. cernua	5	12	5	1.7 ± 0.2	5.7 ± 0.7	78 ± 9	82 ± 5	0.37 ± 0.11	0.27 ± 0.05
G. striata	5	14	3	1.0 ± 0.1	1.5 ± 0.2	71 ± 5	56 ± 5	0.19 ± 0.06	0.21 ± 0.04
S. pectinata-K	5	12	0	0.7 ± 0.1	1.2 ± 0.1	129 ± 3	123 ± 9	0.27 ± 0.13	0.62 ± 0.23
C. canadensis	0	0	4	2.1 ± 0.2	3.0 ± 0.5	70 ± 3	75 ± 2	0.24 ± 0.03	0.32 ± 0.05
C. stricta	0	0	2	0.8 ± 0.0	1.0 ± 0.1	94 ± 3	83 ± 3	0.20 ± 0.10	0.47 ± 0.06
P. arundinacea	1	0	5	0.9 ± 0.1	1.2 ± 0.1	81 ± 7	82 ± 4	0.95 ± 0.26	1.11 ± 0.29
T. latifolia	0	0	5	0.6 ± 0.0	0.7 ± 0.0	135 ± 5	120 ± 6	0.62 ± 0.14	0.53 ± 0.07
S. pectinata-S	5	6	0	1.0 ± 0.1	1.4 ± 0.1	131 ± 20	131 ± 10	0.20 ± 0.08	0.31 ± 0.07

Taxa are listed (by their abbreviations) from most to least sensitive to flooding (see Table 2). NA: data not available.

Table 4
Contributions to sums of squares (given as percentages of total) from general linear models of five response variables

Source	Shoot biomass	Root biomass	Whole-plant biomass	Shoot:root ratio	Final plant height
Taxon	61.6	67.8	65.8	25.7	59.1
Flood Trt	6.2	11.2	9.1	13.9	4.9
Interaction	21.5	11.3	15.0	36.9	15.3
Error	10.7	9.7	10.1	23.5	20.7

All main effects and interactions were significant at $P < 0.0001$. Degrees of freedom: taxon = 16, flood regime = 3, interaction = 48, and total = 339.

significant for all taxa except *B. ciliatus*, *S. pectinata*-Sumner, and *T. latifolia*; and (2) the development of adventitious roots off the stems of 51 out of 85 High treatment plants (60%) encompassing all taxa except *B. ciliatus*, *O. riddellii*, *C. granularis*, and both populations of *Spartina* (Table 3).

Both taxon and treatment effects were significant for percent root airspace ($P < 0.0001$ and $P = 0.0003$, respectively), and there was also a significant taxon × treatment interaction ($P < 0.0001$). Percent root airspace (estimated as the increase in root weight when air was replaced with water) was highly variable within and among taxa, ranging from 5% for *E. maculatum* to 95% for *P. arundinacea* in the Low treatment and from 15% for *O. riddellii* to 111% for *Phalaris* in the flooded treatments (Table 3), but overall, the High treatment had significantly greater root airspace than all other treatments, and *Phalaris* had significantly higher levels of root airspace than the other taxa tested. When grouped by growth form, grasses and graminoids (*C. granularis*, *C. stricta*, and *T. latifolia* in our study) had a higher percent root airspace than broadleaf forbs in the Low treatment and also in the flooded treatments (overall, airspace = 50 ± 5% for grasses and graminoids versus 30 ± 3% for forbs; d.f. = 263, $P = 0.001$).

Taxon flood sensitivity values ranged from a low of 0.09 for *S. pectinata*-Sumner to a high of 0.98 for *B. ciliatus* (Table 2). Shoot, root, and whole-plant biomass production in the Low treatment were significantly and inversely related to flood sensitivity ($r^2 = 0.29$, 0.48, and 0.46, respectively; d.f. = 16, and $P < 0.03$ for all), while shoot:root ratios were significantly positively related to flood sensitivity ($r^2 = 0.53$, d.f. = 16, $P = 0.0009$). Neither height nor root airspace correlated with flood sensitivity.

4. Discussion

We hypothesized that invasive potential of wetland angiosperms would be a function of overall sensitivity to flooding [expressed as: 1 − (mean whole-plant biomass produced in the three flooded treatments)/(mean whole-plant biomass produced in the Low treatment)], and our results indicate that the invasive reed canary grass (*P. arundinacea*) and broadleaf cattail (*T. latifolia*) were among the three most flood-tolerant taxa. Furthermore, both species produced more shoot, root, and whole-plant biomass than nearly all other perennial taxa in the three flooded as well as in the unflooded treatment (Table 5), suggesting that rapid early growth contributes to their flood tolerance and thus allows them to dominate

Table 5
Taxon ranks from highest (1) to lowest (17) for shoot biomass, root biomass, whole-plant biomass, and final plant height

Taxon	Shoot biomass					Taxon	Whole-plant biomass				
	Low	4H/4L	4H/4D	High	Mean rank		Low	4H/4L	4H/4D	High	Mean rank
B. cernua	1	1	13	1	4.0	*B. cernua*	1	1	13	1	4.0
P. arundinacea[a]	2	2	1	2	1.8	*T. latifolia*[a]	2	2	3	2	2.3
C. granularis	3	9	4	15	7.8	*P. arundinacea*[a]	3	3	1	3	2.5
T. latifolia[a]	4	3	6	3	4.0	*C. stricta*	4	4	2	4	3.5
C. stricta	5	4	2	4	3.8	*E. perfoliatum*	5	11	8	6	7.5
S. puniceum	6	10	8	8	8.0	*S. pectinata*-K	6	5	4	7	5.5
C. canadensis	7	6	3	9	6.3	*C. granularis*	7	10	6	15	9.5
S. pectinata-K	8	7	5	7	6.8	*S. puniceum*	8	9	10	8	8.8
G. striata	9	5	7	10	7.8	*G. striata*	9	6	7	11	8.3
E. perfoliatum	10	12	12	6	10.0	*C. canadensis*	10	8	5	9	8.0
A. incarnata	11	11	10	12	11.0	*S. pectinata*-S	11	7	9	5	8.0
S. pectinata-S	12	8	9	5	8.5	*A. incarnata*	12	12	11	10	11.3
H. grosseserratus	13	16	17	13	14.8	*H. grosseserratus*	13	16	17	13	14.8
O. riddellii	14	13	14	16	14.3	*O. riddellii*	14	13	14	16	14.3
S. gigantea	15	14	11	11	12.8	*S. gigantea*	15	14	12	12	13.3
E. maculatum	16	15	15	14	15.0	*E. maculatum*	16	15	15	14	15.0
B. ciliatus	17	17	16	17	16.8	*B. ciliatus*	17	17	16	17	16.8
	Root biomass						Height				
T. latifolia[a]	1	1	2	1	1.3	*H. grosseserratus*	1	16	17	13	11.8
P. arundinacea[a]	2	2	3	2	2.3	*T. latifolia*[a]	2	2	3	2	2.3
B. cernua	3	4	14	5	6.5	*S. pectinata*-S	3	1	2	1	1.8
E. perfoliatum	4	8	5	6	5.8	*S. pectinata*-K	4	3	1	3	2.8
C. stricta	5	3	1	3	3.0	*A. incarnata*	5	4	5	7	5.3
S. pectinata-K	6	5	4	7	5.5	*C. stricta*	6	5	6	6	5.8
G. striata	7	6	7	10	7.5	*S. puniceum*	7	9	4	8	7.0
C. granularis	8	11	10	14	10.8	*P. arundinacea*[a]	8	6	8	5	6.8
S. pectinata-S	9	7	6	4	6.5	*B. cernua*	9	7	14	4	8.5
S. puniceum	10	9	9	9	9.3	*G. striata*	10	10	9	11	10.0
A. incarnata	11	12	11	8	10.5	*C. canadensis*	11	8	7	9	8.8
C. canadensis	12	10	8	11	10.3	*C. granularis*	12	11	11	15	12.3
H. grosseserratus	13	16	17	15	15.3	*S. gigantea*	13	14	10	10	11.8
O. riddellii	14	13	12	16	13.8	*E. perfoliatum*	14	12	12	12	12.5
E. maculatum	15	15	15	13	14.5	*O. riddellii*	15	13	13	16	14.3
S. gigantea	16	14	13	12	13.8	*E. maculatum*	16	15	15	14	15.0
B. ciliatus	17	17	16	17	16.8	*B. ciliatus*	17	17	16	17	16.8

Rankings (1: highest 17: lowest). Taxa are ranked for each of the four treatments and overall ("mean rank"). 4H/4L = 4 High/4 Low; 4H/4D = 4 High/4 Dry.

[a] Taxon is known to be potentially invasive in wetlands.

under a range of hydrologic conditions, at least when nutrients are not limiting. Even when their growth was severely curtailed under the dual stresses of flooding and drought (4 High/4 Dry treatment), *Phalaris* and *Typha* still produced more biomass than all taxa except for the native tussock sedge *C. stricta*. Results for plant height were less straightforward:

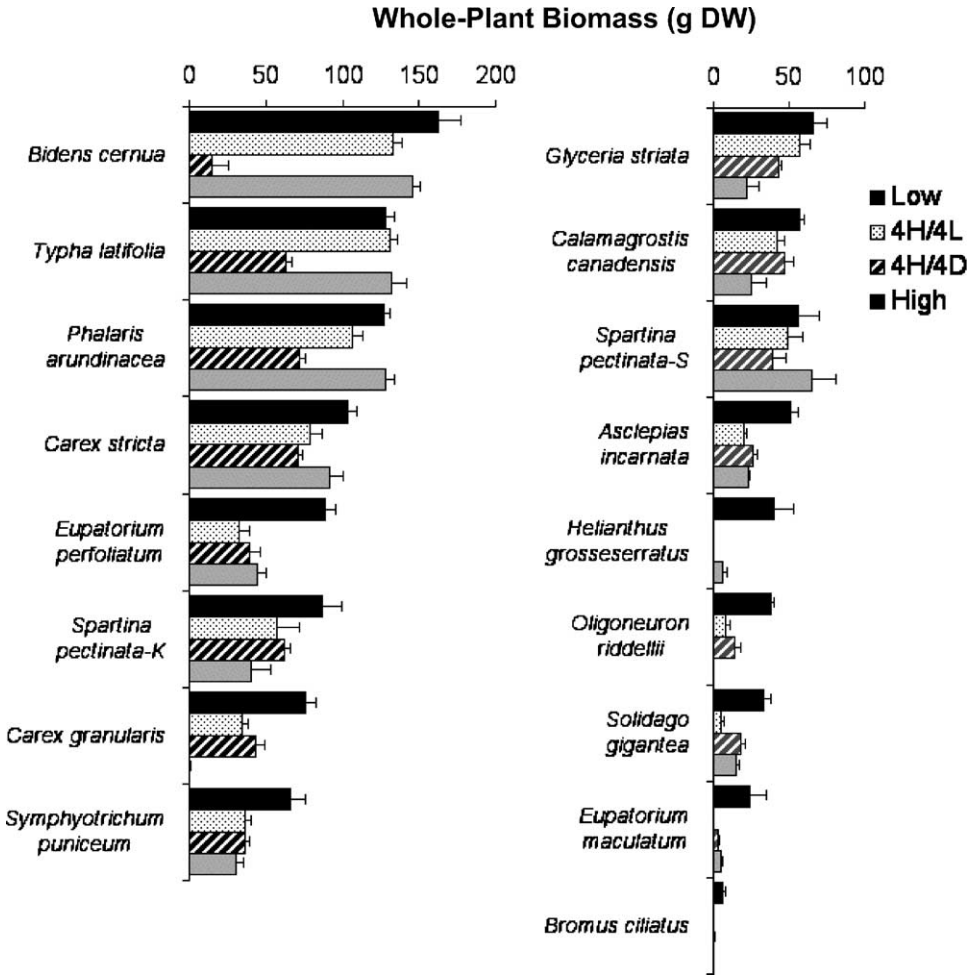

Fig. 2. Summary of whole-plant biomass production for 17 taxa and 4 hydrologic regimes (+S.E. bars, $n = 5$ for each taxon × treatment combination), presented in order of highest to lowest biomass production in the Low treatment.

Typha was the second tallest of the seventeen taxa, but *Phalaris* was only the sixth tallest (Table 5). Nevertheless, height is only one aspect of canopy architecture and dominance; other important characteristics include canopy layering and cover (e.g., Keer and Zedler, 2002), which we did not measure in this study.

In addition to being the two most productive perennial species, *Typha* and *Phalaris* had similar biomass responses to the experimental treatments (Fig. 2). These two species also have similar distributions and ecological strategies. Both are widely distributed in North America, especially in areas characterized by seasonal or permanent surface water (Goslee et al., 1997), and belong to the same functional group: Boutin and Keddy (1993) classified

both species as "Matrix Clonal Dominants" based on a cluster analysis of 27 morphological and life history traits. *Phalaris* and other *Typha* species (e.g., *Typha angustifolia* and *Typha* × *glauca*) are known to form monotypes in wetlands (Galatowitsch and van der Valk, 1995; Galatowitsch et al., 1999), and their occurrence has been linked to stormwater runoff in a landscape-scale study of Minnesota prairie pothole wetlands (Galatowitsch et al., 2000). Our study suggests that the tall invasive competitors *Phalaris* and *Typha* will likely dominate under a wide range of hydrologic conditions, at least if nutrients are abundant, which is a realistic scenario in urban and agricultural landscapes.

In contrast to the invasive taxa, the widespread, noninvasive taxa characteristic of diverse sedge meadows (Curtis, 1959; Kercher et al., 2004) were moderately tolerant of flooding and attained moderate biomass and height, with the exception of the very tall and sometimes very flood-tolerant *S. pectinata*. The only obligate annual in our study, *B. cernua*, was the most productive species in all but the 4 High/4 Dry treatment, a result that helps explain its rapid colonization and dominance of moist, open, nutrient-rich mudflats. Although it was the superior producer of biomass in three out of four treatments, its short life impairs its ability to persist and compete with perennial invasive species.

Using young plants, we found that rapid accumulation of shoot, root, and whole-plant biomass was associated with greater flood tolerance. Rapid growth rates could allow establishing plants to escape submersion and/or afford them greater morphological plasticity in response to flooding (e.g., adventitious root development to escape anoxic conditions in the root zone, as we saw in 12 of the 17 taxa in the High treatment). The taxa that were most sensitive to flooding—including *B. ciliatus*, *C. granularis*, *E. maculatum*, *Helianthus grosseserratus*, and *O. riddellii*—are commonly found in wetlands with lower water tables and/or groundwater-fed, nutrient-poor wetlands (Curtis, 1959; Gleason and Cronquist, 1963; Goslee et al., 1997). These habitat specialists were short and/or poor producers of biomass in the Low treatment, and most failed to produce adventitious roots in the High treatment. Therefore, these taxa will likely experience the most rapid declines in areas that become impounded or experience greater volumes of runoff.

Based on the literature, we predicted a greater amount of root airspace in flood-tolerant plants and increased root airspace for individual taxa in response to flooding (e.g., Kawase and Whitmoyer, 1980; Hook, 1984; Jackson and Drew, 1984; Justin and Armstrong, 1987; Burdick, 1989; Seliskar, 1990). Although we detected no significant relationship between the flood sensitivity index and root airspace, and no significant increase in root airspace due to flooding for individual taxa, grasses and graminoids nearly always tolerated flooding better than the broadleaf forbs, and we found greater levels of root airspace in the former. Of all the taxa we tested, the invasive wetland grass *P. arundinacea* had the highest amount of root airspace, a trait that could allow *Phalaris* to survive, spread, and form monotypic stands in chronically anoxic soils unfavorable for most native wet meadow species.

We predicted shifts in biomass allocation from roots to shoots in response to flooding based on other studies (e.g., Rubio et al., 1995). We found significant increases in shoot:root ratios for all taxa, as predicted, but we also found a strong direct relationship between flood sensitivity and net change in shoot:root ratio—i.e., the flood-tolerant taxa showed very small increases in shoot:root ratios due to flooding, while sensitive taxa showed sometimes dramatic increases in shoot:root ratios due to flooding, primarily from the death of roots. The more consistent allocation patterns in the flood-tolerant taxa,

including the invasives *Phalaris* and *Typha*, may be related to the presence of aerenchyma in these taxa.

The invasive species in this experiment grew better and were more tolerant of hydrologic stresses than nearly all of the noninvasive taxa in the four hydrologic treatments. In another experimental study of the invasive cattail *T. domingensis* and the noninvasive Everglades species *Cladium jamaicense* and *Eleocharis interstincta*, only *Typha* responded positively to increased water depth (15, 30, and 60 cm) by increasing biomass as much as 60% (Newman et al., 1996). However, not all experimental comparisons of invasive and noninvasive species agree with these findings. Miller and Zedler (2003) report equivalent biomass responses of the invasive grass *P. arundinacea* and the noninvasive grass *S. pectinata* propagated from rhizomes and subjected to four hydroperiods and two water depths within experimental pots, with one exception: *Phalaris* grew best and produced more biomass than *Spartina* when flooding alternated weekly with drawdown. However, resources were limiting in this experiment (Miller and Zedler, 2003). Lempe et al. (2001) found no evidence that the invasive *Lythrum salicaria* was more flood-tolerant than five other noninvasive members of the family Lythraceae. Vandersande et al. (2001) report that the invasive *Tamarix ramosissima* was less tolerant of flooding but was more tolerant of elevated salinity levels than four noninvasive native riparian species. Horton and Clark (2001) found that water level declines and drought, conditions that often occur downstream from dams and diversions, favored seedlings of the exotic desert riparian species *Tamarix chinensis* over the native *Salix gooddingii*. Lorenzen et al. (2001) contrasted the growth of a noninvasive (*C. jamaicense*) and invasive (*T. domingensis*) species of the Florida Everglades and found little effect of anoxia on the growth, biomass allocation, and nutrient use efficiency in either species (but see Newman et al., 1996). Clearly, there are few studies comparing the responses of invasive and noninvasive species to stresses, and even fewer that compare different populations of a single species–and our two populations of *Spartina* differed somewhat in flood tolerance. Hence, it is difficult to generalize. More tests comparing the relative responses of invasive and noninvasive taxa to stresses are needed, and the stresses should match levels—including extremes—found in nature.

While tolerance of flashy or chronically-flooded conditions may be one factor that helps explain the invasiveness of *Phalaris* and *Typha*, their superior growth compared to other perennial species under unflooded conditions (and the inferior growth of the habitat specialists across all treatments; Table 5) hints at the importance of other factors—e.g., nutrients—in enabling some plants to become invasive (e.g., Lorenzen et al., 2001; Kercher and Zedler, 2004). Further experimental tests of invasive versus noninvasive wetland taxa under a range of hydrologic regimes should be combined with a range of nutrient levels to elucidate the independent and interacting roles of flooding and nutrients, as well as to determine the thresholds at which noninvasive species are favored over the invasives.

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