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Factors affecting post-control reinvasion by seed of an invasive species, *Phragmites australis*, in the central Platte River, Nebraska

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Abstract Invasive plants, such as *Phragmites australis*, can profoundly affect channel environments of large rivers by stabilizing sediments and altering water flows. Invasive plant removal is considered necessary where restoration of dynamic channels is needed to provide critical habitat for species of conservation concern. However, these programs are widely reported to be inefficient. Post-control reinvasion is frequent, suggesting increased attention is needed to prevent seed regeneration. To develop more effective responses to this invader in the Central Platte River (Nebraska, USA), we investigated several aspects of *Phragmites* seed ecology potentially linked to post-control reinvasion, in comparison to other common species: extent of viable seed production, importance of water transport, and regeneration responses to hydrology. We observed that although *Phragmites* seed does not mature until very late in the ice-free season, populations produce significant amounts of viable seed (>50 % of filled seed). Most seed transported via water in the Platte River are invasive perennial species, although *Phragmites* abundances are much lower than species such as *Lythrum salicaria, Cyperus esculentus* and *Phalaris arundinacea*. Seed regeneration of *Phragmites* varies greatly depending on hydrology, especially timing of water level changes. Flood events coinciding with the beginning of seedling emergence reduced establishment by as much as 59 % compared to flood events that occurred a few weeks later. Results of these investigations suggest that prevention of seed set (i.e., by removal of flowering culms) should be a priority in vegetation stands not being treated annually. After seeds are in the seedbank, preventing reinvasion using prescribed flooding has a low chance of success given that *Phragmites* can regenerate in a wide variety of hydrologic microsites.

Keywords Common reed · Hydrochory · Prescribed flooding · River restoration · Vegetation management

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Introduction

Invasive plant species in rivers have transformed many riparian corridors worldwide by altering vegetation structure and composition, stabilizing dynamic channel features, diminishing flows, and even altering soil chemistry (Richardson et al. 2007). Where spread has been extensive, these changes have reduced the ecosystem services of these rivers diminishing freshwater supplies for rural communities, habitat for endangered species, and recreational use (Zavaleta 2000; Turpie et al. 2008). These lost services motivate attempts to control or eradicate invasive species despite the logistical challenges of mechanical and chemical treatments in or near water and the risk of reinvasion after control (Galatowitsch and Richardson 2005; Shafroth et al. 2005). While the outcomes of most control programs are not formally assessed or reported, available published information suggests that ameliorating the effects of invasive species spread to maintain river functions is not common (Richardson et al. 2007). Where native species have been displaced, invasive species often reinvade before native species recolonize (e.g., Galatowitsch and Richardson 2005). Maintaining dynamic, sparsely vegetated landforms such as point bars, islands and channel banks, and preventing reinvasion can be especially problematic because plants tolerant of high frequency and intense disturbance are typically short-lived species (e.g., annuals), unlikely to pre-empt reinvasion. Moreover, altered flow regimes may favor invasive over native, non-invasive species, triggering reinvasions unless key components of the natural flow regime are re-established (Stromberg et al. 2007). Developing more effective strategies for controlling invasive species on rivers is clearly needed, and will likely only be successful if widespread eradication is possible and if post-control environmental conditions do not favor reinvasion.

The Central Platte River in the US Great Plains is an example of an invaded riverine ecosystem where there is a clear imperative for control, although ambitious efforts to do so have largely yielded only short-term results (Rapp et al. 2012). Several invasive perennials, notably *Phragmites australis*, *Lythrum salicaria*, and *Phalaris arundinacea*, have extensively spread through the active channel (i.e., the portion of the river that is influenced by flowing water), forming dense stands that stabilize banks, point bars, and islands. *Phragmites australis* (common reed) is especially abundant and widespread, often lining the channels in dense, monotypic stands. This coarse perennial grass, which grows to 6 m in height, spreads extensively by rhizomes and stolons. While the causes for the spread of *Phragmites* on the Platte River are not known, it did coincide with a regional drought in the early 2000s (Runge 2007, personal communication). The natural flows of the central Platte River in the Great Plains have been highly altered by water development for irrigation, hydropower production, flood protection, and municipal water supply (Williams 1978; Eschner et al. 1981; NRC 2004). Flood flows, in particular, have decreased markedly. Elsewhere in inland freshwater aquatic systems, low water levels, and the arrival of a non-native genotype have been observed to cause rapid expansion of *Phragmites* (Galatowitsch et al. 1999; Hudon et al. 2005; Lelong et al. 2007; Tulbure and Johnston 2010). *Phragmites* spread on the Central Platte River during a prolonged drought was likely facilitated by increased rates of seedling emergence, vegetative spread and ramet survival.

Phragmites has dramatically increased its distribution across North America in recent decades, most likely due to the ability of a European genotype to capitalize on anthropogenic alterations to aquatic systems (Lelong et al. 2007). Larson et al. (2011) determined that the *Phragmite*s invading the Platte River is of European origin; only scattered, small stands of the North American strain of *Phragmites* are present. European genotypes of *Phragmites* were present on the Platte River as early as 1973 (Larson et al. 2011).

On the Platte River, *Phragmites* invasions have deleterious consequences for wildlife use and have contributed to transforming the active channel of the river. In-stream stabilization by *Phragmites* is constricting the flow of water through stable channels, decreasing sediment transport, and reducing roosting habitat for sandhill cranes (Kessler et al. 2011; Horn et al. 2012). Since 2008, a consortium of government agencies and private conservation organizations has undertaken an extensive control program, treating over 3100 ha with the herbicide Imazapyr in the first 3 years (Johnson 2012). In addition, some of the in-channel areas most critical for crane roosting are tilled to minimize vegetative regrowth. While the program has reduced the severity of the infestation, regular retreatment is necessary. While considerable attention has been paid to improving *Phragmites* management in freshwater and tidal coastal wetland systems (Hazelton et al. 2014 and citations therein), comparable information in riverine systems, such as the Platte River, is lacking.

The spread of *Phragmites australis* is often assumed to be vegetative (from rhizome fragments) because seed production in some populations was reported to be low (e.g., Ailstock et al. 2001; Ishii and Kadono 2002 and references therein). However, recent studies suggest that *Phragmites* does spread by seed (Belzile et al. 2009; McCormick et al. 2010; Kettenring et al. 2011; Albert et al. 2015) and that in some locales non-native *Phragmites* is more likely to spread by seed than native *Phragmites* (Kettenring and Mock 2012). The question of whether or not seed is important to the spread of *Phragmites* on the Platte River is important for improving control strategies. If seeds are contributing to spread, control strategies that focus on preventing seed set and on minimizing seedling establishment should be a high priority for management. Allowing seedbanks of invasive species greatly complicates control efforts by increasing the likelihood of reinvasion over greater distances and longer time frames.

In this paper, we report several aspects of the seed ecology of *Phragmites* potentially linked to post-control reinvasion on the central Platte River in Nebraska, in comparison to other common co-occurring species not considered to be of high management concern. We sought to determine if viable seeds of *Phragmites* were being produced in the central Platte River populations, and if so, to determine if they are being dispersed via water, which could facilitate long-distance transport. We also investigated whether it was possible to reduce colonization by seed using prescribed flooding treatments. We used a combination of observational field studies (i.e., seed viability and seed dispersal) and controlled greenhouse experiments (i.e., seedling response to hydrology) to understand controls on post-control reinvasion of *Phragmites*. The extensive stands of *Phragmites* on the Platte River initially require control efforts be focused on adult plants and preventing clonal spread, but even if this is accomplished, seeds are likely to persist in the river corridor or be dispersed there. Our studies on *Phragmites* seed dynamics are intended to inform comprehensive control programs in riparian habitats.

Methods

Our investigations focused on *Phragmites*-invaded stream reaches on the central Platte River, a major tributary of the Missouri River, between the towns of Lexington and Chapman, Nebraska (US) (Fig. 1). This area was selected for a set of related studies on impacts from invasive alien species and altered hydrology (e.g., Kinzel et al. 2006; Larson et al. 2011). In addition, the vegetation of this section of the Platte River is actively managed by conservation organizations and public agencies seeking to maintain critical habitat for several species of concern (e.g., sandhill cranes, *Grus canadensis,* whooping cranes, *Grus americana*, least terns, *Sternula antillarum*, piping plovers, *Charadrius melodus*).

Seed dispersal

The composition and abundance of viable seed dispersed in the main channel of the River was characterized for six locations using floating aquatic traps (adapted from Middleton 1995). Sites selected were representative of typical channel conditions and accessible. Trapping methods were tested and refined in 2008 on the Platte River. The floating aquatic trap was made from a 10 cm diameter PVC pipe between two 2-l soda bottles and a bag secured to the end of the pipe (Fig. 2). The bag was made from polyester meshtriangular pores with a maximum width of 4.8 mm and length of 5.3 mm).

The design allowed the PVC pipe to float half-way out of the water, so that material floating on the surface of the water was collected inside the mesh bag. Each trap was attached to a rope which spanned the channel and was attached to anchors on the river banks. This rope had enough slack so that the trap was able to remain in the water at both peak and low flows.

Seed traps were deployed every 6-weeks from May 19 to November 24 2009 and in March (25–26) 2010. The number of locations ranged from 2 to 6, depending on flow conditions; in March 2010, two locations were sampled due to high flows; five locations were sampled after June due to low flows. Seeds were collected for 24 h for each trap set. Flow rates for the Central Platte River at the sampling times were estimated by averaging the USGS gauge record data from the two stations within the study area (Kearney and Grand Island) for the dates the traps were in place (USGS Water-Data Reports). Upon removal of the trap from the river, the mesh bags were placed individually into plastic bags. Traps were cleaned after each use. Germination assays were performed by placing each seed trap sample on sterile media, 3:1

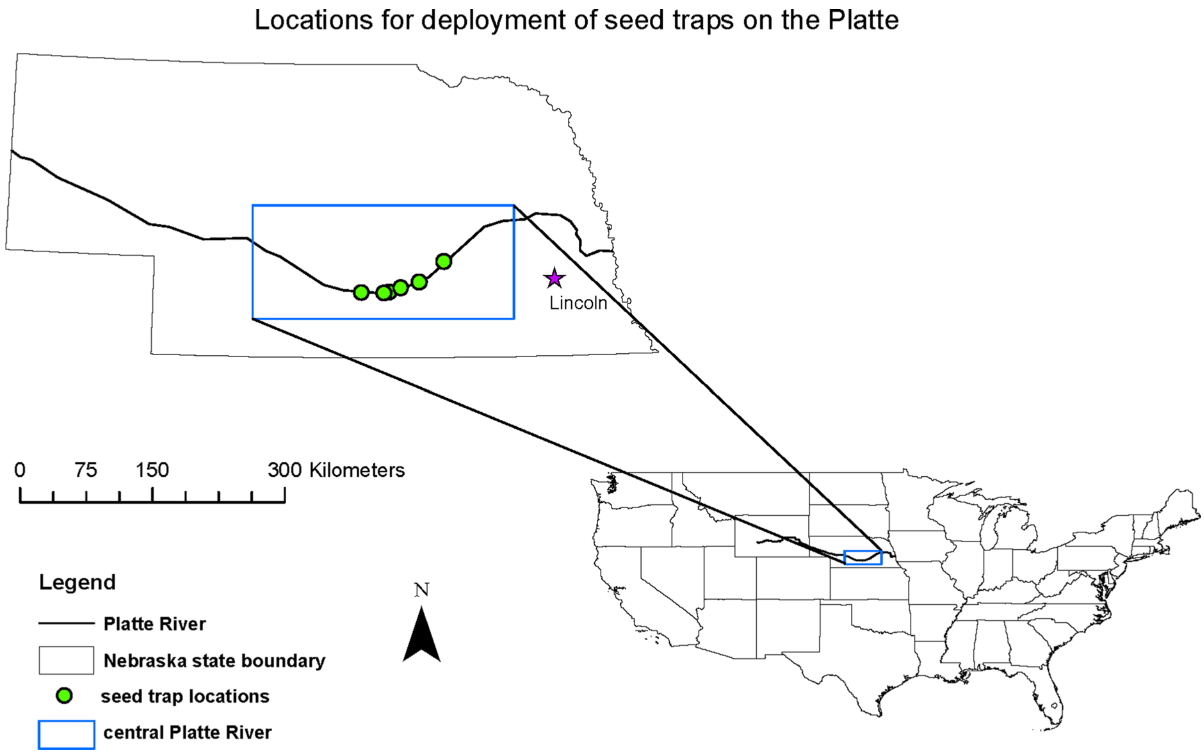

Fig. 1 The study area location on the Central Platte River, Nebraska (USA)

sand-soil mix and grown under saturated conditions for 4 months.

Seed viability and establishment

We conducted a greenhouse experiment to determine if *Phragmites* seed can germinate and establish under the range of hydrological conditions typical of channel margins in the study area. We compared the establishment of *Phragmites* to three co-occurring species, *Echinochloa crus-galli, Eragrostis pectinacea*, and *Phalaris arundinacea*. *Echinochloa* and *Eragrostis* are short-lived species; *Phalaris* is a clonal perennial species.

Seed viability and germinability were estimated from seeds collected within the study area, acquired for controlled greenhouse experiments. We collected seeds from *Echinochloa, Eragrostis,* and *Phalaris* in August, 2008. Because *Phragmites australis* seed ripens in October and November on the central Platte River, we collected seed heads from several locations weekly during October and November, 2008. Each weekly sample was a volume of approximately 27,000 cm^3. Seeds of all species were inspected for fill and maturity under 40× magnification. All seeds that appeared mature and filled were removed and combined into a single seed lot. Seeds were air dried at room temperature and stored for no more than 30 days prior to determining viability and germinability. One sample of approximately 100 seeds for each of the four species was tested for viability using the tetrazolium assay (Peters 2000); a second sample of 100 seeds was tested for germinability following Elias et al. (2006). Both estimates were made at the point of seed ripening and not intended to account for after-ripening (i.e., dormancy); therefore they were not cold-stratified or otherwise treated to promote after-ripening. Pure live seed (PLS) for each species was determined based on estimates of viability or germinability, whichever was greater (PLS = number of filled seed x proportion viable or germinable) (Elias et al. 2006).

Seed collected from the study area was placed on the surface of sterile Platte River sediment and grown in shallow containers (20 × 20 × 7 cm) for 4 months under long-day (16 h), full-spectrum lights, with air temperatures fluctuating between 24 C (day) and 13 C

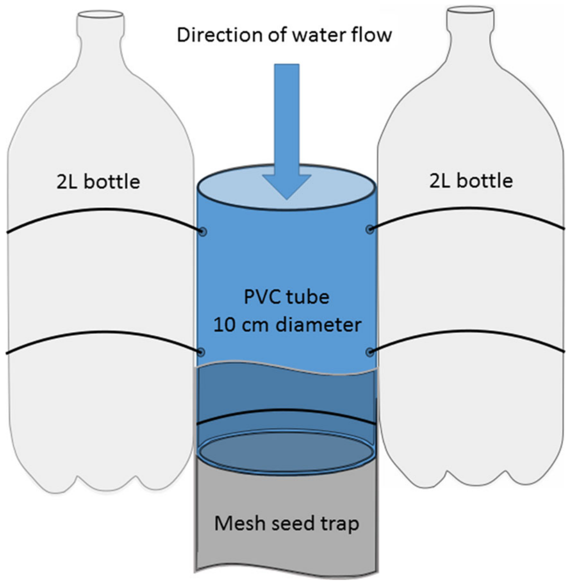

Fig. 2 Floating aquatic traps used to characterize seed transport was characterized for 6 locations on the Platte River. The floating aquatic traps were designed to float half-way out of the water, so that material floating on the surface of the water was directed into a PVC tube (10 cm diameter) and collected in a mesh bag (triangular pores with a maximum width of 4.8 mm and length of 5.3 mm)

(night). Seventy-two containers were each seeded with 100 seeds (PLS) of a single species that had been cold-stratified for 60 days.

The containers were arranged in 91.5 × 107 cm hydrologic treatment cells, which were rubber-lined partitions of greenhouse benches. Each cell was used to treat seedling flats with one of six flooding conditions: 1. Early season-short duration, 2. Early season-long duration, 3. Late season-short duration, 4. Late season-long duration, 5. Hydrocycling, 6. Constant. A flood event consisted of a water level increase of 4 cm (Fig. 3). Early season floods were applied 2 weeks post-planting; late season flooded were applied 2 weeks post-planting. Floods of short and long durations maintained high water condition for seven and fourteen days, respectively. The hydrocycling treatment mimicked conditions created by power generation on the Platte River, which was 10 h of high water (+4 cm) and 14 h at base water levels each day. For the constant treatment, water levels did not change during the experiment.Treatments were randomly assigned to cells so that each was situated on all four greenhouse benches.

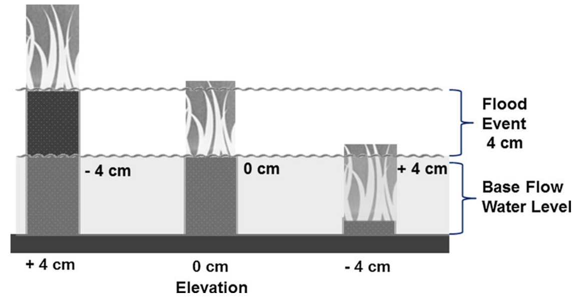

Fig. 3 The effects of flooding on seedling establishment were investigated in a controlled experiment conducted in rubber-lined sections of greenhouse benches. Within a section cell, seedling flats were situated in one of three baseflow water levels: −4, 0, +4 cm. Flood treatments consisted of raising the water level 4 cm above the original elevation (0 cm) for different durations and at different times

Within a hydrologic treatment cell, seedling flats were situated in one of three base flow water levels (i.e., relative to soil surface elevation): −4 cm, 0, +4 cm. Base flow water levels represent the different hydrologic conditions occurring along the elevational gradients of riverbanks. Base flow water level treatments were created by elevating flats on risers of varying heights (Fig. 3). In total, there were eighteen hydrological treatments (i.e., full crossed factorial design), each with four replicates. Establishment rates were based on the number of stems present in each flat after 4 months.

The data for each species were analyzed with a general linear model, following a randomized block design, considering effects of greenhouse bench (3 df), flooding regime (5 df), base flow water levels (2 df), flooding regime x base flow water levels (10 df). The analysis was performed in SAS (Version 8.2 2008). Effects were considered statistically significant using a threshold of $p < 0.05$. Individual means were compared with least squared means test when the overall main effect was significant.

Results

Seed dispersal

A total of 27,781 germinable seeds were collected from traps deployed in the river channel, based on the seedling emergence assay. Nearly all (92 %) were identified to genus or species. Six taxa accounted for

80 % of all trapped, germinable seeds: *Cyperus* sp., *Cyperus esculentus, Lythrum salicaria, Cyperus erythrorhizos, Conyza canadensis,* and *Phalaris arundinacea* (Table 1). *Cyperus esculentus, Lythrum salicaria*, and *Phalaris arundinacea* are considered invasive perennial species (USDA, NRCS 2014). Compared to these three invasive taxa, *Phragmites* seeds were much less numerous and detected at fewer sites. Nineteen *Phragmites* seeds were collected at two locations on the Platte River whereas the other three species were detected at all collection sites and had seed collection totals ranging from 751 to 11,539.

Seasonal patterns of seed dispersal varied among these four invasive taxa (Table 2). Dispersal of *Phragmites* seed was only detected in March and nearly all *Phalaris arundinacea* seed (97 %) dispersed in June. In contrast, seeds of *Lythrum salicaria and Cyperus esculentus* dispersed throughout the March–November collection period, although relatively few seeds of each species (1–2 %) dispersed in March. Flow rates on the Central Platte River ranged from a mean flow rate of 7.67–43.98 $m^3 s^{-1}$, with the lowest rates observed in May and August and the highest rates in March, June and November.

Seed viability and establishment

Most filled seed from the Platte River collections for all four species (*Phragmites, Phalaris, Echinochloa, Eragrostis*) were viable (52–79 %, Table 3).

Table 1 Total number of germinable seeds collected in seed traps based on seedling emergence assay. Data for *Phragmites australis* is highlighted in bold text

Species	Number of sites	Number of seedlings	Species	Number of sites	Number of seedlings
Cyperus sp.	6	11,539	*Bidens tripartita*	6	52
Cyperus esculentus	6	6799	*Agalinus tenuifolia*	5	51
Lythrum salicaria	6	1420	*Fragaria virginiana*	6	36
Cyperus erythrorhizos	6	1006	*Taraxacum officinale*	6	36
Conyza canadensis	6	781	*Populus deltoides*	5	35
Phalaris arundinacea	6	751	*Veronica anagallis-aquatica*	6	30
Eclipta prostrata	6	693	*Mentha arvensus*	6	29
Ranunculus sceleratus	6	253	*Boehmeria cylindrica*	6	28
Cyperus squarrosus	6	236	*Plantago major*	6	28
Polygonum sp.	5	194	*Cyperus diandrus*	4	23
Polygonum persicaria	5	166	*Oenothera biennis*	6	23
Polypogon monspeliensis	6	166	*Amaranthus* sp.	4	21
Echinochloa crus-gallii	5	112	*Potentilla* sp.	5	20
Juncus torreyi	6	105	***Phragmites australis***	**2**	**19**
Juncus bufonis	5	98	*Rumex maritimus*	5	17
Bidens sp.	4	94	*Polygonum pensylvanicum*	2	15
Panicum capillare	4	93	*Verbena hastata*	4	14
Rumex sp.	5	82	*Eragrostis pectinacea*	4	12
Chenopodium sp.	5	79	*Gleditsia triacanthos*	4	10
Leersia oryzoides	6	75	*Polygonum lapathifolium*	2	10
Lycopus americanus	6	66	Unknown forb	6	2106
Lippia lanceolata	6	63	Unknown grasses	6	200

Seeds were collected six times (6 week intervals, May–November 2009 and March 2010) in traps deployed at a maximum of six sites. Taxa with 10 or more seeds detected are shown here (data from 34 species are not shown—Taxa with <10 seeds*: Acer* sp., *Ambrosia artemiisifolia, Artemisia cf biennis, Bidens cernua, Bidens frondosa, Bromus secalinus, Bromus* sp., *Chenopodium album, Coreopsis* sp, *Echinochloa muricata, Echinochloa* sp., *Eleocharis acicularis, Eleocharis* sp, *Helianthus* sp., *Juncus* sp., *Lactuca serriola, Melilotus officinalis, Oxalis* sp., *Plantago rugelii, Plantago* sp., *Poa* sp., *Rotala ramosior, Rumex crispus, Rumex salicifolia, Scutellaria lateriflora*, *Senecio vulgaris, Solidago* sp., *Spartina pectinata, Thlaspi arvense, Ulmus americana, Ulmus* sp, *Urtica dioica*, *Verbascum thapsus*, *Xanthium strumarium*)

Table 2 Seasonal patterns in the numbers of germinable seeds trapped of *Phragmites* and the three invasive taxa with the highest seed abundance, based on seedling emergence assays

			Numbers of germinable seeds			
Collection month	Flow rate cms mean (SD)	No. locations	*Phragmites australis*	*Phalaris arundinacea*	*Lythrum salicaria*	*Cyperus esculentus*
March	39.51 (6.12)	2	19	1	10	177
May	9.12 (4.63)	6	0	5	400	1803
June	43.98 (5.21)	6	0	730	366	2107
August	7.67 (0.77)	5	0	1	104	1447
September	21.16 (1.61)	5	0	10	234	955
November	43.76 (25.43)	5	0	9	306	310
Total no. seeds			19	751	4420	6799

Seeds were collected six times (6-week intervals, May–November 2009 and March 2010) in traps deployed at 2–6 locations, depending on suitability of flow conditions for sampling. Mean flow rates are from USGS gauge records at Kearny (06770200) and Grand Island (06770500) NE on sampling dates (USGS 2014a, b)

Table 3 Seed viability estimated from a TZ (Tetrazolium) assay and germinability based on seedling emergence under controlled conditions (moist filter paper, 14 days)

Species	TZ viability (%)	Germinability (%)
Phragmites australis	66	25
Phalaris arundinacea	52	65
Echinochloa crus-galli	79	1
Eragrostis pectinacea	53	3

Each estimate (viability or germability for a species) is based on a single lot of 100 seeds

Germinability estimates varied substantially among the four species; less than 5 % of filled seed of *Echinochloa* and *Eragrostis* germinated, in contrast to *Phragmites* (25 %) and *Phalaris* (65 %).

For all species in the controlled greenhouse study (*Phragmites, Phalaris, Echinochloa*, and *Eragrostis*), both base flow water levels and flooding regime affected seedling emergence ($p < 0.05$, all main effects). Because seedling emergence rates were very low for *Eragrostis* (32 seedlings overall, 70 % of flats with no seedlings), the data are not normally distributed and so are not discussed further. *Phalaris* had the highest rates of seedling emergence, ranging from a mean of 6.8 seeds per pot (high base flow water level, hydrocycling) to 135 (low base flow water level, constant flooding) (Table 4). *Phragmites* seedling emergence varied from a mean of 5 (high base flow water level, hydrocycling) to 87 (mid base flow water level, constant flooding). Seedling emergence was considerably lower for *Echninochloa*, 0.5 (high base flow water level, hydrocyling) to 19.5 (low base flow water level, late/short flooding).

Seedling emergence of all three species was suppressed at the highest baseflow water level, which was persistently inundated, regardless of flooding regime (Table 4). For *Phragmites*, small differences in elevation resulted in large differences in seedling emergence. An elevational difference of only 4 cm from the mid- to high- base flow water levels resulted in a >80 % decrease in seedling establishment (Fig. 4). The effect of base flow water level was less pronounced for *Echinochloa* and *Phalaris*. *Echinochloa* seedling emergence at highest base flow water level was 33.8 % of mid-water levels and 25 % of low water levels. *Phalaris* seedling emergence at the highest base flow water levels was approximately half of mid- and low water levels (58.3 and 50.9 %, respectively).

Comparing the effects of flooding regimes, seedling emergence was suppressed to the greatest extent for *Phalaris* and *Echinochloa* by hydrocycling; for *Phragmites*, suppression was greatest under the early/long flooding regime, followed by hydrocycling (Table 4). Flooding regimes supporting the highest seedling emergence were constant inundation for *Phragmites* and *Phalaris*, and early/short flooding for *Echinochloa*. On average, about twice (2.1×) as many *Phragmites* seedlings emerged under constant flooding compared with early, long-duration flooding (Fig. 5). A similar difference (2.3×) between constant

Table 4 Mean number of seedlings emerging at different baseflow water levels and flooding regimes in controlled greenhouse study (out of 100 PLS)

Mean no. seedlings	Baseflow water levels (cm)			
Flooding regime[a]	High (−4)	Mid (0)	Low (+4)	LS mean
Hydrocycling				
Phragmites	5.00	40.00	50.25	31.75
Phalaris	6.75	47.50	85.00	46.42
Echinochloa	0.50	7.75	11.25	6.50
Early-long				
Phragmites	6.50	39.75	30.50	25.58
Phalaris	80.00	71.50	92.50	81.33
Echinochloa	5.50	9.50	13.75	9.58
Early-short				
Phragmites	13.20	50.75	41.00	35.00
Phalaris	59.75	101.00	95.00	85.25
Echinochloa	4.25	12.25	16.75	11.08
Late-long				
Phragmites	12.50	49.25	75.25	45.67
Phalaris	60.50	107.75	107.50	91.92
Echinochloa	4.50	11.25	13.25	9.67
Late-short				
Phragmites	11.25	65.50	72.75	49.83
Phalaris	47.25	113.00	120.50	93.58
Echinochloa	5.75	11.50	19.50	12.25
Constant				
Phragmites	10.50	77.75	76.75	55.00
Phalaris	69.25	114.25	134.75	106.08
Echinochloa	1.50	12.75	13.25	9.17
Least squares means				
Phragmites	9.83	53.80	57.75	
Phalaris	53.92	92.50	105.87	
Echinochloa	3.67	10.83	14.63	

[a] Hydrocycling = 10 h high water levels, 10 h base levels daily, Early-long = High water levels 2 weeks post-planting, 14 d duration, Early-short = High water levels 2 weeks post-planting, 7 d duration, Late-long = High water levels 6 weeks post-planting, 14 d duration, Late-Short = High water levels 6 weeks post-planting, 7 d duration. Control = no change in water levels

and hydrocycling flooding regimes was observed for *Phalaris*, and for *Echinochloa* between early, short - duration flooding and hydrocycling (1.7×).

Discussion

This study demonstrates the importance of understanding seed regeneration dynamics in the control of invasive species in riverine systems, even for species capable of aggressive clonal spread. Regeneration from seed likely contributes to the spread and post-control reinvasion of *Phragmites* on the Platte River in Nebraska, based on the production of viable seeds, as well as the capacity of these seeds to regenerate under a wide-range of hydrologic conditions. Consequently, strategies devised to control non-native *Phragmites* in riverine systems should include prevention of viable seed production and planned treatments of re-emerging seedlings following removal of mature vegetation. Studies of the fate of *Phragmites* seedbanks are needed to determine how long the reinvasion risk from seed is likely to persist after the eradication of adults in the population.

This research establishes that *Phragmites australis* populations in the central Platte River corridor are producing viable seeds. We observed that *Phragmites* seeds do not mature until very late in the fall (November) and that more than half of ripe seeds are viable. Production of viable *Phragmites* seed has been

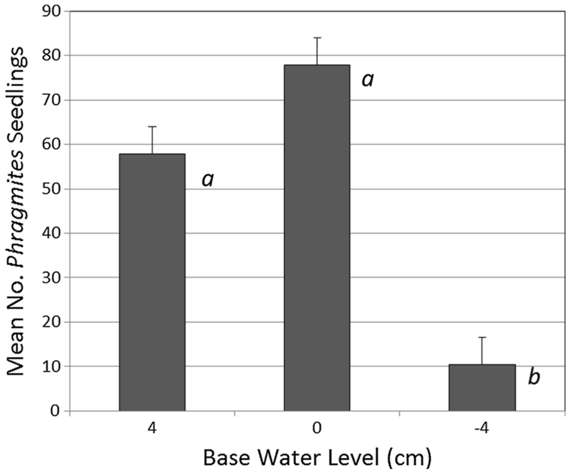

Fig. 4 The mean number of seedlings establishing (out of a maximum of 100 PLS) at each baseflow water level (standard errors shown). Significantly different means shown as *a,b*

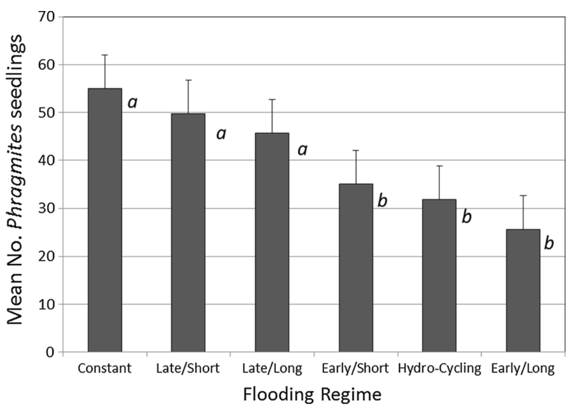

Fig. 5 The mean number of seedlings establishing (out of a maximum of 100 PLS) for each flooding treatment (standard errors shown). Hydrocycling = 10 h high water levels, 10 h base levels daily, Early-long = High water levels 2 weeks post-planting, 14 d duration, Early-short = High water levels 2 weeks post-planting, 7 d duration, Late-long = High water levels 6 weeks post-planting, 14 d duration, Late-Short = High water levels 6 weeks post-planting, 7 d duration, Constant = no change in water levels. Significantly different means shown as *a,b*

reported to be limited by self-incompatibility and latitude. Kettenring et al. (2011) observed that new *Phragmites* colonies (European genotype) on the Chesapeake Bay produce seeds with very low viability (<1 %), while established populations produced abundant, viable seeds (5–21 %). Over time, colonies founded by seeds of a single genotype receive influxes of seed from other genotypes, overcoming reproductive barriers of self-fertilization (McCormick et al. 2010; Kettenring et al. 2011). European genotypes have been present in the central Platte River since at least 1973 (Larson et al. 2011), apparently providing sufficient time for colonization and mixing of genotypes along the river corridor, promoting viable seed production. The quantities of seeds produced by *Phragmites* populations on the Platte River, not measured in this study, could, however, be limited by latitude. Several studies report that northern populations of *Phragmites* in Europe, Asia and North America often flower so late that winter dieback commences before many seeds ripen (e.g., Gervais et al. 1993; McKee and Richards 1996; Ishii and Kadono 2002). The timing of seed ripening we observed on the Platte River seems likely to be affected by winter dieback, potentially affecting the overall abundance of *Phragmites* seed produced.

Phragmites seed is dispersed by the Platte River, although compared to three other perennial invasive species, exhibits a relatively low rate of seed movement via water. Our in-river seed collections yielded 16 *Phragmites* seeds, compared to 751 seeds for *Phalaris arundinacea*, 1420 for *Lythrum salicaria*, and 6799 for *Cyperus esculentus*. There are several possible explanations for these findings. First, *Phragmites* transport may be limited by low buoyancy. Compared to other wetland species, *Phragmites* seed loses its capacity to float relatively quickly in both stagnant and moving water (van den Broek et al. 2005). Approximately half of *Phragmites* seeds lose buoyancy within a month whereas for high buoyancy species, most seeds maintain the capacity to float for 6 months or more. Systematic trials of seed buoyancy have not been published for *Phalaris, Lythrum* or *Cyperus*. Second, *Phragmites* seed may be relatively less abundant than other invasive species in the river corridor because of lower seed production or less persistent seedbanks. Temporal patterns of seed collections suggest that secondary dispersal of seeds (i.e., from seedbanks) into the river is more important for *Lythrum* and *Cyperus* than for *Phragmites* and *Phalaris.* Seeds are moving in the river at relatively similar rates from March to November for the former, but duration of seed transport is much shorter (i.e., about a month) for the latter. *Lythrum* and *Cyperus* are reported to form persistent seedbanks although information on the longevity of seeds under field conditions is lacking (Lapham and Drennan 1990; Welling and

Becker 1990). The viability of *Phragmites* and *Phalaris* seed in soil is presumed to be low, as is typical of grasses; however, high density seedbanks are known to occur (e.g., Galatowitsch and Biederman 1998; Hazelton et al. 2014), which suggests seeds persist for at least a few years. Third, hydrochory may be a relatively unimportant seed dispersal mechanism for *Phragmites* compared to other pathways. Of the four prevalent invasive perennial species, only *Phragmites* has plumed seed, which confers the ability to efficiently disperse via wind.

Low rates of seed movement via water observed in this study could also stem from under-detection. *Phragmites* seed may be transported in the river at higher rates than estimated because conditions (i.e., ice, cold water) did not permit sampling from December to February. *Phragmites* has been reported to release its seeds during winter and early spring (Haslam 1973), suggesting most dispersal occurs in winter and our collections under-estimate river transport. However, although it is likely that the amount of *Phragmites* seed moving in the river is higher than reported here, it is still likely lower than for other prevalent invasive perennial species in the Platte River corridor, which store seeds in channel sediments for long periods of time and do not rely on wind-dispersal for long-distance transport.

In general, most of the seeds transported by the Platte River are invasive perennial species and short-lived species (introduced and native). For the twelve species with the highest rates of water dispersal in the Platte River (i.e., those with more than 100 seeds collected), three are invasive perennials (*Cyperus esculentus, Lythrum salicaria, Phragmites*), five are native annuals or short-lived perennials (*Cyperus erythrorhizos, Conyza canadensis, Eclipta prostrata, Ranunculs sceleratus, Cyperus squarrosus*) (USDA, NRCS 2014). Four species are introduced annuals or short-lived perennials (*Polygonum persicaria, Polypogon monspeliensis, Echinochloa crus-galli*); only one species, *Juncus torreyi*, is a long-lived native perennial. The species composition of the most-frequently collected seeds in the river is not surprising, given invasive, long-lived perennial species and short-lived species typically produce large quantities of seed. This pattern is, however, consistent with recent vegetation changes on historically sparsely vegetated riverbanks and sandbars of the Platte River. Prior to the arrival of invasive perennials such as *Lythrum salicaria* and *Phalaris arundinacea*, seeds stranding on riverbanks and sandbars were primarily short-lived species, which allocate little biomass to their roots, do not spread vegetatively, and typically do not live more than a year or two. These short-lived species would not have formed dense stands capable of resisting scouring by floods. So, although *Phragmites* has been the focus of active management on the Platte River, our results indicate that the interactions between the river and adjacent lands have changed because of the arrival of several invasive perennial species. Most of the plant colonizers entering the river and delivered back to land downstream are now long-lived invasive species, which tend to stabilize river landforms. Moreover, the channels of large, braided rivers with high frequency flood disturbances and a predominance of depositional surfaces, favor plants with strategies exhibited by these invasive species: water dispersal and seed regeneration (Bornette et al. 2008). Breaking this self-reinforcing cycle through weed control requires management strategies that address multiple species, the seed dynamics of these species, as well as the adult stages of their populations (Hazelton et al. 2014).

Following control of adult populations of *Phragmites*, preventing seeds from establishing is critical, although our studies suggest this will be challenging to accomplish even if river flows could be manipulated for vegetation management. Seedling establishment of both *Phragmites* and *Phalaris* is very sensitive to base flow water levels, with small differences in the hydrologic setting creating large differences in recolonization risk. This sensitivity to elevation is most pronounced for *Phragmites* where, on average, a 4 cm drop in base flow water levels increased seedling establishment by as much as 83 %. However, because seeds are stranded across broad elevational gradients, corresponding to high and low water levels associated with fluctuations in discharge, microsites favorable to *Phragmites* seedling establishment will not limit recolonization, unless flood events diminish the suitability at these optimal elevations.

Experimental flooding treatments show that timing of prescribed flood events is particularly important for reducing *Phragmites* seedling establishment. Flood events occurring 2 weeks after planting, which coincided with the beginning of seedling emergence, reduced establishment by as much as 59 % compared to flood events occurring 4 weeks later. *Phragmites* establishment is less sensitive to flooding duration than timing. These results suggest that flow releases effective for limiting seedling establishment need to be carefully timed to the phenology of seedling emergence of *Phragmites* on sandbars and river banks to achieve desired results. Further investigation is needed to determine if emergence is sufficiently synchronous to be able to time events and thus significantly limit establishment. It is important to recognize that the greatest reduction in colonization at the most favorable microsites (i.e., base elevation above the normal water level) still allowed 30 % of the viable seeds to establish. So, while these experiments demonstrate that prescribed flooding has potential to reduce seedling establishment, more research is needed to develop a prescription capable of a greater reduction (i.e., near zero) and to determine if this prescription is feasible to implement.

The current invasive species control program on the central Platte River is similar to programs on wetlands elsewhere in North America including recurrent treatments of dense stands of adult vegetation with herbicides and/or mechanical removal (Hazelton et al. 2014). The results of this study indicate that without follow-up treatment of regenerating seedlings, any reduction in *Phragmites* extent will be very temporary since *Phragmites* is spread not only by vegetative propagules, but also by seed, on the Platte River. We also found that seedling establishment is not so sensitive to changes in hydrology that modest changes in flooding regimes can be used as a form of control. Once seeds populate the sediments of river corridors, as they do in the Platte River, reducing reinvasion by seed will likely require multiple treatments (chemical or mechanical, depending on site conditions) to control emerging seedlings, as well as depletion of seedbanks by preventing the addition of new seeds to the sediment. This reduction of seed availability requires removal of all flowering heads (likely by mowing) prior to seed ripening. Thus, adequate control of *Phragmites* on a large river cannot be pursued on patchworks of land tracts that are chosen annually, but needs to be comprehensively addressed on a river-wide basis to reduce reinvasion risk by seed.

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