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NONNATIVE *PHRAGMITES AUSTRALIS* INVASION INTO UTAH WETLANDS

Andrew Kulmatiski¹, Karen H. Beard², Laura A. Meyerson³, Jacob R. Gibson², and Karen E. Mock²

ABSTRACT.—*Phragmites australis* (Cav.) Trin. ex Steud. (common reed), already one of the world's most widespread plant species, has realized rapid range expansion in coastal wetlands of North America in the past century, but little is known about *P. australis* range expansion in inland wetland systems. We used genetic analyses, aerial photographs, field surveys, and a greenhouse experiment to study the extent and mechanism of nonnative *P. australis* invasion of Utah wetlands. We collected and genetically analyzed 39 herbarium samples across the state and 225 present-day samples from northern Utah's major wetland complexes. All samples collected before 1993 and all samples collected outside the major wetlands of northern Utah, including some as recent as 2001, were identified as native (haplotypes A, B, D, and H). Only 10 (4%) of the present-day samples were native, each from small, discrete, low-density stands; the remaining samples were nonnative (haplotype M). Our earliest nonnative sample was collected near the Great Salt Lake in 1993. Around the Great Salt Lake, which contains 40% of Utah's wetlands, *P. australis* cover has increased from 20% to 56% over the past 27 years—an increase that appears attributable to the nonnative strain. In a 3-month-long greenhouse experiment, the nonnative haplotype grew taller, had more aboveground biomass, and had a greater above- to below-ground biomass ratio than the native haplotypes regardless of nitrogen, phosphorus, or water availability. Nonnative *P. australis* is rapidly invading the wetlands of northern Utah. Areas in Utah where the native *P. australis* remains should be identified and protected.

Key words: Bear Lake, competition, Great Salt Lake, greenhouse experiment, haplotype, inland wetlands, invasive plants, native vegetation, nitrogen, phosphorous, Phragmites, Utah Lake.

RESUMEN.—*Phragmites australis* (Cav.) Trin ex Steud (carrizo), una de las especies de plantas más ampliamente distribuida en el mundo, se ha extendido rápidamente en los humedales costeros de Norteamérica en el último siglo, pero se conoce poco sobre la expansión de *P. australis* en sistemas de humedales del interior. Utilizamos análisis genéticos, fotografías aéreas, estudios de campo y un experimento en invernadero para examinar el alcance y el mecanismo de la invasión de la variedad no nativa de *P. australis* en los humedales de Utah. Recolectamos 39 muestras de herbario a lo largo del estado y 225 muestras actuales de los mayores complejos de humedales en el norte de Utah, y las sometimos a un análisis genético. Todas las muestras recolectadas antes de 1993 y las que se recolectaron fuera de los mayores humedales del norte de Utah, siendo las más recientes del 2001, fueron identificadas como nativas (haplotipos A, B, D y H). Solo 10 (4%) de las muestras actuales fueron nativas, todas de pequeños carrizales separados con baja densidad; las restantes fueron no nativas (haplotipo M). Nuestra muestra no nativa más antigua se recolectó cerca del Gran Lago Salado en 1993. Alrededor del Gran Lago Salado, el cual contiene el 40% de los humedales del estado de Utah, la cubierta de *P. australis* incrementó del 20% al 56% durante los últimos 27 años, un aumento que parece atribuirse a la variedad no nativa. En un experimento de invernadero de tres meses, el haplotipo no nativo creció más alto, tenía más biomasa sobre el nivel de la tierra y una mayor proporción de biomasa sobre el nivel de la tierra por biomasa subterránea que los haplotipos nativos sin importar la disponibilidad de nitrógeno, fósforo o agua. El haplotipo no nativo de *P. australis* está invadiendo rápidamente los humedales del norte de Utah. Las áreas en Utah en donde las variedades nativas permanecen deben ser identificadas y protegidas durante el manejo de carrizos.

Phragmites australis (Cav.) Trin. ex Steud. (common reed) is a tall (2–4 m), clonal grass that grows in freshwater and brackish wetlands and is one of the most widespread plant species on earth (Holm et al. 1977). This species has been present in North America for at least 10,000 years (Niering and Warren 1980); however, over the past 100–150 years its distribution and abundance have expanded rapidly (Chambers et al. 1999, Rice et al. 2000, Saltonstall 2002, Lelong et

al. 2007). The recent range expansion has been typified by dense monocultures that decrease habitat quality for some avifauna and other wetland species (Benoit and Askins 1999, Chambers et al. 1999, Bertness et al. 2002). *Phragmites* expansion is of particular management concern in northern Utah, which is part of the Western Hemisphere Shorebird Reserve Network and serves as a stopover location for 35 million birds in the Pacific Flyway (Aldrich and Paul 2002).

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Several explanations have been invoked to explain recent *P. australis* expansion in North America. Initially, researchers suggested that anthropogenic disturbances, such as soil disturbance and nutrient addition, increased *P. australis* growth (Van Der Toorn and Mook 1982, Marks et al. 1994, Meyerson et al. 2000, Bertness et al. 2002, Silliman and Bertness 2004, Chambers et al. 2008). Later, strong evidence suggested that the introduction of an aggressive nonnative strain explained the rapid expansion, particularly throughout the northeastern United States (Saltonstall 2002, 2003a). Disturbance also has been shown to disproportionately improve growth of the nonnative *P. australis* strain in relation to the native strain (Bertness et al. 2002, Minchinton and Bertness 2003, Jodoin et al. 2008, Park and Blossey 2008; but see Saltonstall and Stevenson 2007). Other potential explanations include allelopathic secretions from the nonnative *P. australis* (Rudrappa et al. 2007) and the potential for native and nonnative strains to hybridize (Meyerson et al. 2010). The relative importance of these mechanisms remains unresolved, especially in noncoastal wetlands.

While little is known about inland wetland populations (but see Wilcox et al. 2003, Jodoin et al. 2008), research on the expansion of *P. australis* in North America has focused on Atlantic coastal populations. One study reviewing herbarium (historical) and present-day samples across the United States suggests that inland wetlands were invaded by the nonnative strain after the 1960s (Saltonstall 2002). Other recent reports also suggest that *P. australis* is becoming unusually dense and expanding rapidly in many Utah wetlands, particularly along the shores of the Great Salt Lake and surrounding area (Cross and Fleming 1989). While the rapid expansion has not yet been quantified, local land managers suggest that it began during flooding events which created large mudflats in the 1980s (Grierson personal communication). However, the expansion also coincided with increasing human populations, as well as with a 5-fold increase in P concentration and a 10-fold increase in N concentration in invaded waters (Naftz et al. 2000, Gerner 2003). Which combination of factors contributes to the recent expansion remains unclear because native and nonnative strains can be difficult to distinguish based on morphological characteristics (Saltonstall 2002), and because so many conditions including nonnative invasion, high water levels, and increasing

nutrient concentrations are associated with the expansion in Utah.

With a focus on Utah's 3 largest lakes, the objectives of this study were to (1) investigate the invasion history of nonnative *P. australis* across the state, (2) determine the current extent of native and nonnative *P. australis* cover, and (3) assess factors potentially contributing to *P. australis* spread. Herbarium samples from 1875 to the present were genetically analyzed to describe the historical occurrence of native and nonnative haplotypes. Present-day distribution and relative abundance of nonnative and native haplotypes were characterized for Utah's 3 largest lakes: the Great Salt Lake, Utah Lake, and Bear Lake. These 3 bodies of water support 44% of wetland coverage in Utah, with the Great Salt Lake, alone, representing 40% of the coverage in Utah (Fry et al. 2009). To determine the change in historical and present-day *P. australis* cover, we analyzed Great Salt Lake aerial photographs from 1977 and 2004. Finally, a greenhouse experiment determined if changes in soil moisture status or nutrient loading associated with anthropogenic activities over the past 30 years may have contributed to *P. australis* range expansion.

METHODS

Genetic Analyses

Herbarium samples were used to determine the timing and extent of the invasion of the nonnative haplotype across the state of Utah. At the time of this study, the S.L. Welsh Herbarium at Brigham Young University (BYU) and the Intermountain Herbarium at Utah State University (USU) contained 54 and 29 *P. australis* specimens, respectively (Appendix). All samples that were considered of reliable quality (i.e., were green) and that contained sufficient material for amplification and restriction analysis were included. A total of 39 herbarium specimens were genetically analyzed: 32 specimens from BYU and 7 from USU (Appendix; Fig. 1).

To determine the present-day extent of native and nonnative *P. australis*, leaf samples were collected at 225 *P. australis* occurrence points from the Great Salt Lake, Utah Lake, and Bear Lake. Points were located every 500 m along continuous wetland vegetation, regardless of the width of vegetation, though private property prevented access to some locations. In total, 77 *P. australis* samples were collected along Utah

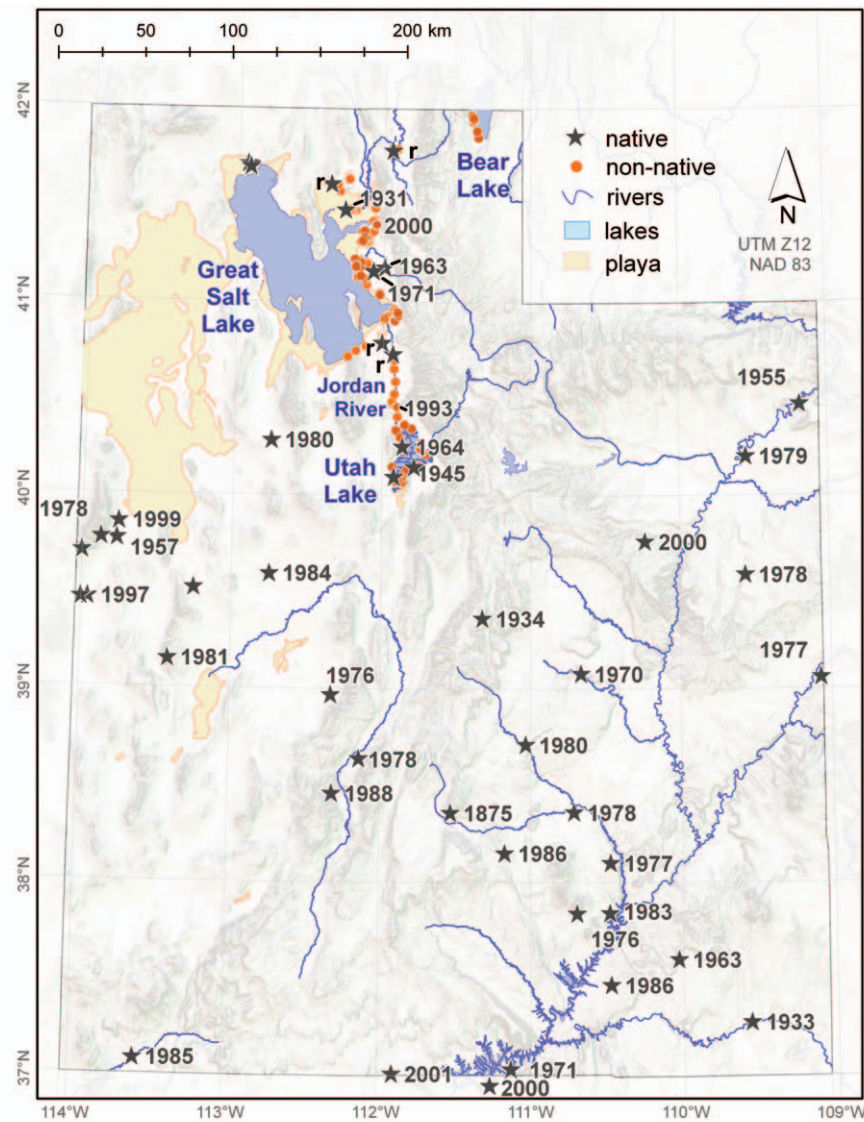


Fig. 1. Native and nonnative *Phragmites australis* distribution in Utah. Sampling dates are indicated next to herbarium specimens through 2001. Symbols without sampling dates represent present-day samples (2000–2006). A lowercase *r* adjacent to sampling points indicates where rhizomes were collected for the greenhouse experiment.

Lake in November 2005, 137 along the Great Salt Lake and Jordan River in August 2006, and 11 along Bear Lake in May 2007 (Fig. 1).

Leaf samples were cut into 1 × 2-cm pieces and field-collected samples were immediately preserved in paper envelopes containing silica gel desiccant. DNA was extracted using Qiagen DNEasy 96 Plant Kits following the manufacturer's protocol (Valencia, CA). Isolated genomic DNA provided a template in polymerase chain

reactions (PCR) that amplified 2 noncoding regions of the chloroplast genome: (a) *trnLb*—a segment of the intergenic spacer region between *trnT* (UGU) and *trnL* (UAA) (Taberlet et al. 1991, Saltonstall 2002) and (b) *rbcL*—a segment of the intergenic spacer region between *rbcL* and *psaI* (Saltonstall 2001, 2003b). Reaction products were used as templates in subsequent restriction fragment analyses (Saltonstall 2003b) that distinguished native and nonnative haplotypes.

Following native and nonnative haplotype determination, sequencing of the *trnLb* and *rbcL* amplicons was conducted on a subset of the extracted samples (17 field-collected nonnative, 4 field-collected native, and 5 historical native samples) by using protocols of Saltonstall (2002) to identify specific haplotypes. To optimize amplification, the *rbcL* forward and reverse primer was redesigned using PrimerSelect (DNASTAR® Lasargene; 5'-TTGCTCGTGAAGTAAT), and the PCR annealing temperature was modified from Saltonstall's (2002) original protocol for both regions to 54 °C for both primer sets. The amplicons were sequenced at the University of Rhode Island using an Applied Biosystems 3130xl Genetic Analyzer. A combined alignment for each region was created using SeqMan and aligned using Megalign 8.0.2 (Lasargene) software. The alignments were then compared to previously identified haplotypes in GenBank (*rbcL*: AF457382-402; *trnLb*: AY016324-328, AY016332-335, and AY714215-216).

Aerial Photography

To determine *P. australis* ground cover in wetlands surrounding Utah's 3 largest lakes, we determined total wetland area for each lake. Total wetland area for the Great Salt Lake was estimated as the "emergent herbaceous wetland" land-cover class in the National Land Cover Dataset (NLCD) (Fry et al. 2009). Total wetland area for Utah Lake and Bear Lake (often <30 m wide) was visually classified using aerial photographs (2004 National Agricultural Imagery Program [NAIP]) because the NLCD is limited to a 30-m resolution.

Present-day extent of *P. australis* was determined using ground truthing and visual inspection of NAIP images. Ground-referenced points included the 225 *P. australis* points where sampling was conducted and the 60 *P. australis*-free points (*Typha latifolia* L., *Schoenoplectus lacustris* [L.] Pella, and *Scirpus maritimus* L.) located every 500 m along continuous wetland vegetation. In total, there were 37 *P. australis*-free points along the Great Salt Lake and Jordan River, 20 along Utah Lake, and 3 along Bear Lake. In NAIP images, *P. australis* appeared to be darker and taller than other common wetland species, and arranged in circular patterns; thus, we were able to confidently identify *P. australis* in the images. *Phragmites australis* stand characteristics were delineated on images, and the

aerial extent of the stands was determined by using GPS-verified distances. Wetland area covered by *P. australis* was then divided by total wetland area to determine the percent cover of wetland for each lake.

After using present-day data for training, we were able to determine *P. australis* cover on historical images. Historical images from 1966, 1977, and 1982 were inspected, but only one image from 1977 was of sufficient quality to clearly delineate *P. australis* coverage. This 1977 image was available for one section of the Great Salt Lake, but 21% of the wetlands associated with the Great Salt Lake, Utah Lake, and Bear Lake were included (Fig. 2).

Greenhouse Experiment

A 3-month-long greenhouse experiment was conducted to measure plant growth of native and nonnative strains under high- and low-resource conditions. To conduct the experiment, 16 trays of twenty 1.2-L pots (320 pots total) were established and defined by redwood dividers. Each pot received 1.2 L of washed sand and 50 mL of soil slurry from a local, *Phragmites*-free wetland (111°56'35.3"W, 41°47'6.57"N). The slurry provided microbial inocula.

Results from the genetic assay were used to identify 4 native and 4 nonnative populations from which rhizomes were collected on 27 February 2007 (Fig. 1). The 4 sites in each category were spaced from 5 to 150 km apart. Paired native and nonnative stands within each site were located within 3 km of each other. On 1 March 2007, rhizomes were rinsed with water and cut into 4.0 ± 0.01 g pieces that included 1 or 2 nodes. Half of the pots in each tray were randomly assigned native rhizomes and half were randomly assigned nonnative rhizomes. Two to 3 replicates from each population were included per tray. Each pot received three 4-g rhizome pieces from the same population.

Each tray of 20 pots was randomly assigned to 1 of 4 treatment levels: control (10 trays), high N (2 trays), high P (2 trays), and low water content (2 trays). Control treatments were designed to reflect N and P concentrations in freshwater streams, and high N and P treatments were designed to reflect concentrations observed in the Great Salt Lake and Utah Lake (Loving and Waddell 2000, Gerner 2003). At the beginning of the experiment, all pots received a modified Hoagland's solution that provided $0.64 \text{ mg} \cdot \text{kg}^{-1}$ N and $0.08 \text{ mg} \cdot \text{kg}^{-1}$ P.

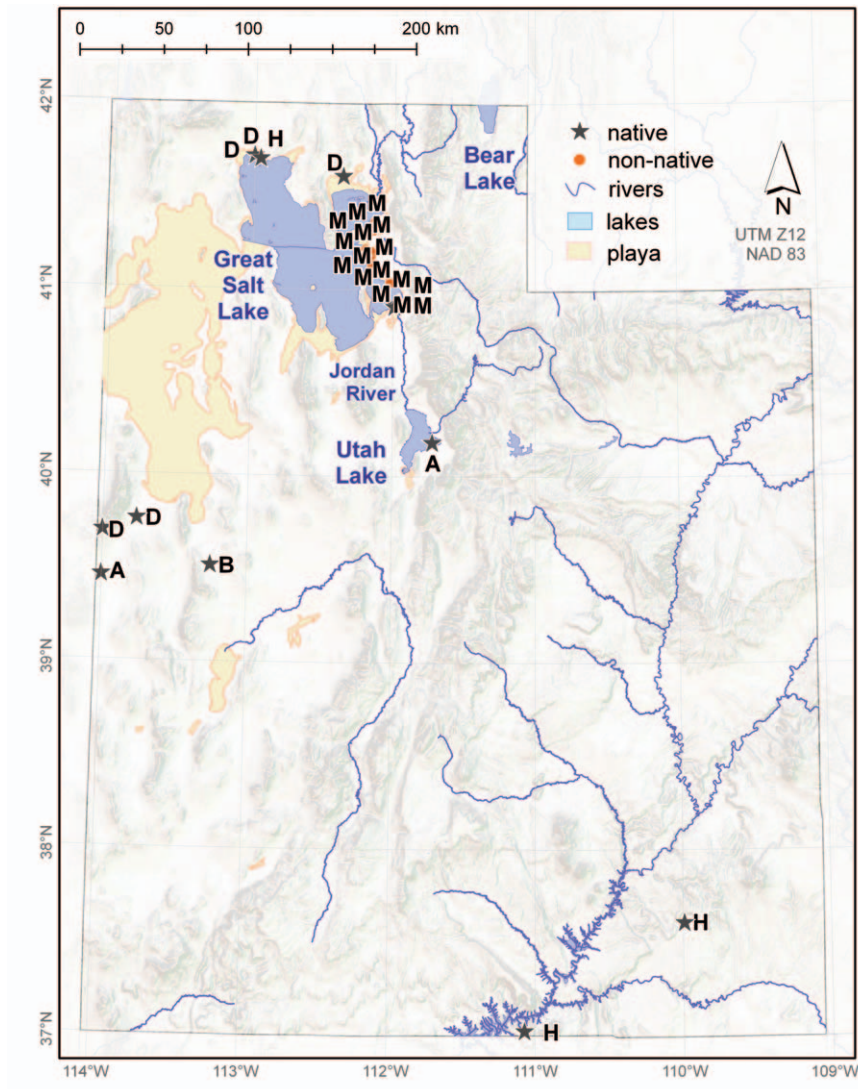


Fig. 2. Native (A, B, D, and H) and nonnative (M) *Phragmites australis* haplotypes for present-day and historical samples from Utah.

The high-N treatment pots received an additional 20 mL of a $714 \text{ mg} \cdot \text{L}^{-1}$ potassium nitrate solution or 3.3 mg N ($2.7 \text{ mg N} \cdot \text{kg}^{-1}$ soil). The high-P treatment pots received 20 mL of a $45 \text{ mg} \cdot \text{L}^{-1}$ potassium phosphate solution or 0.29 mg P ($0.25 \text{ mg P} \cdot \text{kg}^{-1}$ soil). In the low-moisture trays, a 10-mm hole was drilled halfway down each pot to allow the plants to grow in unsaturated soil. Plants were grown under natural greenhouse light conditions, and temperatures varied between $15 \text{ }^\circ\text{C}$ and $25 \text{ }^\circ\text{C}$. Pots were surface watered as

needed throughout the experiment to maintain saturated soils.

During weeks 3 and 5, all pots received additional doses (100 mL) of a modified Hoagland's solution. At the end of the experiment (1 June 2007), maximum height, height of each stem, and number of stems for each pot were recorded. Then all plant parts were removed from pots, rinsed with water until free of soil material, and oven dried at $70 \text{ }^\circ\text{C}$ until biomass remained constant. At that point, values of above- and belowground dry biomass were recorded.

TABLE 1. Land-cover classifications for the 3 major lakes of northern Utah. Herbaceous wetland area for the Great Salt Lake calculated from the National Land Cover Database. Herbaceous wetland areas for Utah Lake and Bear Lake, and *Phragmites australis* cover estimated from National Agriculture Imagery Program 2004 images.

Lake	Herbaceous wetlands (ha)	<i>Phragmites</i> cover (ha)	<i>Phragmites</i> cover (%)
Bear Lake	370	40	11
Great Salt Lake	25,050	8630	34
Utah Lake	2080	890	41

Data Analysis of Greenhouse Experiment

Using ANOVA for 3 experimental factors in a split plot design with subsamples, we assessed the effects of treatment, origin, and population on the following response variables: maximum height, number of shoots, aboveground biomass, belowground biomass, and above- to belowground biomass ratio at the end of the experiment. Trays were defined as the whole-plot unit and treatments as whole-plot factors (control, N, P, and water). Subplot factors were origin (native or nonnative) and population, where population was nested within origin; subplot factors were assigned to sets of pots within a tray. Multiple pots within each tray of a given population were designated as subsamples.

The model assumptions of normality and homogeneity of variance were examined by using Kolmogorov–Smirnov tests and graphical analyses of residuals. To meet assumptions of normality and homogeneity of variance, height, aboveground biomass, and belowground biomass were square-root transformed and stems were log transformed. Comparisons of means clarified treatment and population effects as well as interactions. A Tukey–Kramer adjustment decreased experiment-wide type I errors, and $P < 0.05$ was considered significant. Analyses were computed using the MIXED procedure in SAS/STAT for Windows®, release 9.1.3 (SAS Institute, Inc., Cary, NC).

RESULTS

Genetic Analyses

In total, 264 *P. australis* samples were collected and genetically analyzed for native and nonnative haplotype determination. Analyses were conducted on 39 herbarium samples collected across Utah from 1931 to 2006 (Fig. 1) and 225 present-day samples collected from 2005 to 2007: 137 from the Great Salt Lake and

Jordan River, 77 from Utah Lake, and 11 from Bear Lake. Haplotypes determined for an additional 23 samples from Saltonstall (2002), including one from 1875 and 22 from 2000, were also included in our analyses, so that our study included all known genetically analyzed samples from Utah.

All herbarium samples collected across Utah before 1993 and all samples collected outside the major wetlands of northern Utah, including some as recent as 2001, were identified as native (Fig. 1). Only 10 (4%) of the 225 present-day samples found within Utah's wetlands were native (Fig. 1); however, no native samples were found in Bear Lake. Each of these 10 samples was found in small, discrete, low-density stands (<0.5 ha), but several of these stands were clustered, resulting in 6 general areas where native stands were found. A large set of native stands (2 ha) was found associated with freshwater springs in the northwest corner of the Great Salt Lake. Another large set of native stands (18 ha) was found on the remote north shore of the Great Salt Lake. Two small (10-m²) stands were found on channelized sections of the northern end of the relatively polluted Jordan River on the outskirts of Salt Lake City. One small (<500-m²), low-density stand was encountered in a remote area on the southwestern shore of Utah Lake, and one very small stand (<6 m²) was located along a roadside in Cache Valley.

DNA was extracted from 26 of the 264 samples and identified to specific haplotype based on *trnLb*, *rbcL*, or *trnLb* + *rbcL* amplicon sequence data. Of these samples, five were herbarium samples identified as native haplotypes A ($n = 2$), D ($n = 1$), and H ($n = 2$) (Fig. 2). An additional 5 present-day samples (collected 2006) were identified as native haplotypes D ($n = 4$) and H ($n = 1$), and the remaining 16 present-day samples were identified as nonnative haplotype M (Fig. 2). One present-day sample from Saltonstall (2002) was identified as native haplotype B (Saltonstall unpublished data).

Aerial Photography

Based on the 2004 aerial photographs, *P. australis* dominated approximately 34% (8610 ha) of wetlands (25,050 ha) surrounding the Great Salt Lake, 41% (860 ha) of wetlands (2080 ha) surrounding Utah Lake, and 11% (40 ha) of wetlands (370 ha) surrounding Bear Lake (Table 1; Fig. 3).

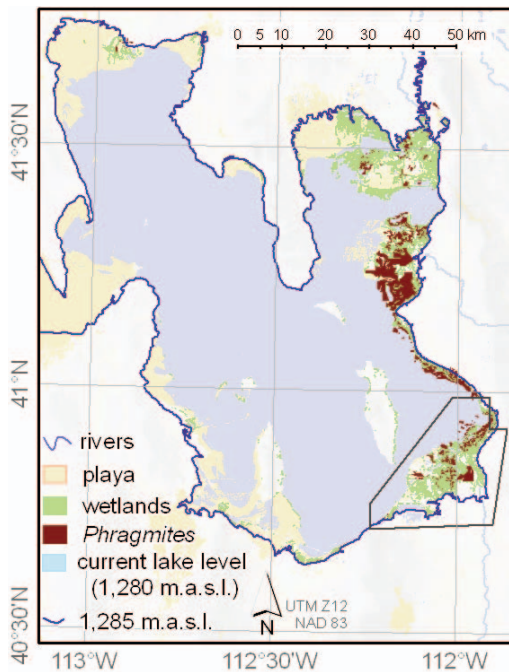


Fig. 3. Current *Phragmites australis* distribution around the Great Salt Lake. The estimate was determined from visual inspection of 2004 National Agricultural Imagery Program images and ground inspection of 285 *P. australis* and *P. australis*-free points. The polygon in the lower right-hand corner indicates the extent of the 1977 aerial photographs used to determine historical *P. australis* abundance.

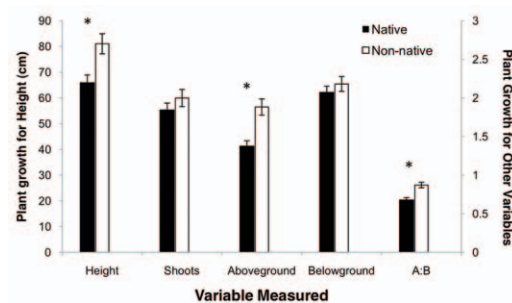


Fig. 4. Mean plant growth responses of native and non-native *Phragmites australis* haplotypes in a 3-month greenhouse experiment. The response variables are maximum plant height per pot in centimeters (height), number of shoots per pot (shoots), dry mass of aboveground plant parts in grams (aboveground), dry mass of belowground plant parts in grams (belowground), and ratio of above- to belowground biomass (A:B). For each measure, significant differences are indicated with an asterisk ($P < 0.05$).

The 1977 aerial photograph captured 5887 ha around the Great Salt Lake and showed 1200 ha

(20.4%) of this area covered by *P. australis*. The 2004 photograph of the same area showed 3320 ha (56.4%) of *P. australis*. Herbarium samples from this area were not available, but herbarium samples taken in 1963 and 1971 near this area (within 25 km) were of the native haplotype (Fig. 1). All present-day samples collected from the area were nonnative.

Greenhouse Experiments

Only 3 of the 320 pots had sprouted plants in the first 3 weeks of the study. Rhizome sprouting rapidly increased following the second nutrient addition at week 3. At the termination of the experiment, 67% of the pots had plants growing in them.

Regardless of treatment, aboveground growth of nonnative-haplotype plants was greater than that of native-haplotype plants (Fig. 4). More specifically (Table 2), nonnative plants grew taller, produced more aboveground biomass, and had a higher above- to belowground biomass ratio than native plants. There was no significant difference between native and nonnative plants in the number of stems produced or in belowground biomass (Table 3).

There was no treatment effect of N addition, P addition, or water reduction on any of the plant growth variables (Tables 2, 3). And the treatment \times origin interaction term was not significant (i.e., treatments did not affect native or nonnative plant growth differently as a whole; Table 3). There were population-level above- and belowground biomass differences (Table 3); however, population differences were not included in our original study objectives and are not discussed further.

DISCUSSION

Phragmites australis (cav.) Trin. ex Steud. now covers nearly 10,000 ha (35%) of the wetlands in northern Utah (the Great Salt Lake, Utah Lake, and Bear Lake). Because 44% of the wetlands in Utah are located in the large wetland complexes of northern Utah (Fry et al. 2009), *P. australis* now covers a significant portion of all wetland habitats in the state. While *P. australis* has been present in North America for the past 10,000 years and in Utah's wetlands since at least 1875 (the earliest record), its recent increase appears to be occurring through introduction of a nonnative strain. The aggressiveness of the nonnative strain has

TABLE 2. Final least-squares means (SE) for plant growth responses of *Phragmites australis* grown in the 3-month greenhouse experiment.

Treatments	Height (cm)	Shoot number (#)	Aboveground biomass (g)	Belowground biomass (g)	Aboveground: belowground	Survivorship
Native						
Control	72 (5.9)	1.9 (0.18)	1.5 (0.15)	2.2 (0.12)	0.67 (0.06)	60%
Drier	55 (13)	1.7 (0.39)	1.1 (0.34)	1.7 (0.27)	0.66 (0.14)	70%
N addition	69 (12)	1.6 (0.38)	1.5 (0.32)	1.9 (0.25)	0.79 (0.13)	80%
P addition	45 (12)	1.6 (0.38)	1.2 (0.32)	1.8 (0.24)	0.70 (0.13)	80%
Nonnative						
Control	82 (6.0)	2.3 (0.18)	1.9 (0.15)	2.1 (0.12)	0.90 (0.06)	65%
Drier	71 (13)	1.6 (0.39)	1.9 (0.34)	2.3 (0.27)	0.77 (0.14)	70%
N addition	85 (12)	2.3 (0.38)	1.8 (0.32)	1.9 (0.25)	0.88 (0.13)	80%
P addition	62 (13)	1.5 (0.40)	1.8 (0.35)	2.2 (0.28)	0.93 (0.14)	70%

TABLE 3. ANOVA results showing fixed effects of treatment (drier, N addition, P addition, and control), origin (native or nonnative), population nested within origin, and their interactions on growth parameters of *Phragmites australis* in the greenhouse experiment. Significant ($P < 0.05$) results are shown in bold.

Source	df	F	P
Height (cm)			
Treatment	3, 11.3	1.78	0.2081
Origin	1, 67.9	6.62	0.0123
Treatment \times origin	3, 68.6	1.09	0.3597
Population (origin)	3, 64.8	0.87	0.5188
Treatment \times population (origin)	18, 62.8	1.08	0.3887
Shoots (#)			
Treatment	3, 11.9	1.18	0.3578
Origin	1, 60.4	1.02	0.3164
Treatment \times origin	3, 60.9	0.99	0.4018
Population (origin)	6, 59.2	1.52	0.1885
Treatment \times population (origin)	18, 57.7	0.6	0.8821
Aboveground (g)			
Treatment	3, 11.5	0.18	0.9074
Origin	1, 62.2	7.83	0.0068
Treatment \times origin	3, 62.7	0.45	0.7166
Population (origin)	6, 61.3	2.53	0.0297
Treatment \times population (origin)	18, 60.2	1.04	0.4274
Belowground (g)			
Treatment	3, 10.6	0.85	0.4969
Origin	1, 69.9	1.01	0.3187
Treatment \times origin	3, 70.2	1.49	0.2242
Population (origin)	6, 67.4	3.89	0.0022
Treatment \times population (origin)	18, 65.3	0.76	0.7335
Above: belowground			
Treatment	3, 11.9	0.2	0.8955
Origin	1, 63.8	8.49	0.0049
Treatment \times origin	3, 64.2	0.58	0.6303
Population (origin)	6, 63.2	2.24	0.0505
Treatment \times population (origin)	18, 62.2	0.84	0.6433

been well-documented in the northeastern United States (Saltonstall 2002), and the results of this study suggest that it is similarly aggressive in inland wetlands.

Our earliest detection of nonnative specimens in Utah was a sample taken between Utah Lake and the Great Salt Lake (i.e., the Jordan

River) in 1993 near Camp Williams, a military installation (Fig. 1). The next herbarium sample taken from this area in 2000 was also nonnative. Herbarium samples vouchered in 1963, 1964, and 1971 from the same region were all native (Fig. 1), suggesting a rapid and dramatic shift from native to nonnative dominance between

1971 and 1993 around the Great Salt Lake. Because most herbarium sampling is limited and biased, it is possible that the nonnative strain was present in Utah before 1993. We suggest that the nonnative haplotype first appeared in Utah during the 1960s or 1970s and began to expand in the 1980s. Evidence for our suggestion is (1) the rapid appearance of the nonnative *P. australis* across North America after 1960 (Saltonstall 2002), (2) the rapid increase in cover observed between the 1977 and 2004 aerial photographs, (3) anecdotal accounts of rapid *P. australis* growth around Utah Lake and the Great Salt Lake in the 1980s (Grierson personal communication), and (4) allowance of a time lag between the arrival and spread of nonnative *P. australis* (Williamson 1996).

Our data suggest that the rapid expansion of *P. australis* cover in northern Utah can be attributed to the nonnative strain. *Phragmites australis* nonnative stands currently have a substantial presence around the Great Salt Lake, Utah Lake, and, to a lesser degree, Bear Lake. Our results showed that the nonnative strain made up 96% of the present-day samples from northern Utah, and, in a direct measure of percent cover change from images, *P. australis* increased 36% (range 20%–56%) between 1977 and 2004 around the Great Salt Lake. All herbarium samples collected near this area in the 1960s and 1970s were native, whereas all area samples collected in and after 2004 were nonnative. It is possible that the nonnative *P. australis* strain occurred in the area prior to 1977, and that the native strain remained in the area after 1977, but was unsampled.

All herbarium samples collected anywhere in Utah prior to 1993 were the native strain. All samples collected outside of the northern wetlands, even those collected recently (1997 [1], 1999 [1], 2000 [2], and 2001 [1]), were also native. This study did not focus on present-day sampling outside of the northern wetlands, so it is unclear whether the nonnative *P. australis* strain is also invading those more remote areas. The 5 samples listed above suggest that at least some stands of native *P. australis* remain across the state.

The most extensive native stands found in present-day samples were on uninhabited north and northwest shores of the Great Salt Lake. The 2 native stands found within the Salt Lake City limits covered areas less than 20 m² and contained fewer than 500 stems each (A.

Kulmatiski personal observation). Herbarium sample descriptions from across the state and our observations indicate that native stands typically associate with small springs and narrow streambeds, covering areas of 0.5 ha or less. Other researchers have also noted that the native strain rarely dominates a community, often does not form a monoculture (Saltonstall and Stevenson 2007), and, by nature of their small population size, may be increasingly vulnerable to eradication.

Our research identified 3 native haplotypes (A, D, and H) not previously identified in Utah but identified in other parts of the southwestern United States (Saltonstall 2002, Saltonstall et al. in press). The only native haplotype previously described in Utah was haplotype B (Saltonstall 2002). Our study shows that haplotype diversity in Utah is higher than previously described, and may be even greater assuming sampling was too limited. Control efforts (i.e., burning, flooding, herbicide) applied to nonnative stands, such as those that have occurred around the Great Salt Lake, may harm native stands, which contain higher genotypic diversity (i.e., native haplotypes A, D, and H) than nonnative stands (haplotype M).

Greenhouse Experiment

The greenhouse experiment was conducted to determine growth responses of native and nonnative strains and if nutrient addition and soil saturation may have played a role in the expansion of nonnative plants in Utah. In our experiment, nonnative plants outperformed native plants regardless of conditions, a result that was similar to results from other greenhouse studies comparing native and nonnative growth patterns (Vasquez et al. 2005, League et al. 2006, Saltonstall and Stevenson 2007). Similar to League et al. (2006), we found this response in stem height, aboveground biomass, and above- to belowground biomass ratio. League et al. (2006) attributed the greater allocation of aboveground resources to greater root or rhizome efficiency or higher quality reserves in the nonnative strain.

Because of increased N and P levels in many Utah lakes, and because the native *P. australis* is often found perched above the water table (A. Kulmatiski personal observation, Amsberry et al. 2000, Minchinton and Bertness 2003), we investigated growth responses of native and nonnative *P. australis* to increased N, increased P,

and drier soils. Strain growth did not vary significantly in N- and P-enriched soil or in drier environments compared to control treatments. This result is quite different than results from other laboratory and field experiments, which show that the nonnative strain has strong responses to increased nutrients (Bertness et al. 2002, Minchinton and Bertness 2003, Rickey and Anderson 2004) or that the native has a stronger growth response to nutrient additions than the nonnative (Saltonstall and Stevenson 2007).

We expected that both strains would respond positively to nutrient enrichments. Potential explanations for our results are (1) that nutrients were nonlimiting because of fertilizer additions at weeks 3 and 5 and/or (2) that nutrient addition treatments were not great enough to elicit a response. In support of the first potential explanation, our above- to belowground biomass ratio was greater than that reported in a similar rhizome study—a result suggesting that soil resources were not limiting in our experiment (League et al. 2006). However, in support of the second potential explanation, most other studies added much more N and P in their treatments. For example, Saltonstall and Stevenson (2007) added 100 times more and Rickey and Anderson (2004) added 200 times more N per kg soil than we did, and Saltonstall and Stevenson (2007) added 730 times more P per kg soil than we did. Our treatments simulated observed high nutrient concentrations in waterways around the Great Salt Lake (Gerner 2003); however, it may be that plants experience different concentrations in the field and that nutrient-addition treatments should be reconsidered.

There are other factors that may have influenced our greenhouse experiment results. The pots used in our experiment were smaller compared to those used in other *P. australis* container experiments (Vasquez et al. 2005, League et al. 2006, Saltonstall and Stevenson 2007), although our above- and belowground biomass measurements suggest that plants were not more root-bound. Sample sizes for native and nonnative strain comparisons were greater than those for treatment comparisons, but trends in our data do not suggest addition of N and P increased growth of either strain. The addition of 3 rhizome pieces to each pot limited our ability to determine the number of propagules per plot. It also precluded us from collecting separate root and rhizome weights in order to assign

categorical belowground biomass allocation, where differences between native and nonnative strains have been observed (League et al. 2006). Finally, our experiment only considered native and nonnative strains of *P. australis*; more general conclusions cannot be made concerning the importance of eutrophication or soil saturation to nonnative haplotype invasion, particularly because our experiment did not examine responses of other native species (e.g., *Scirpus maritimus*) (as in Minchinton et al. 2006, Morris et al. 2008, Zhao et al. 2008).

The nonnative *P. australis* strain is rapidly spreading throughout northern Utah and now makes up a large component of the wetland landscape. Based on available data, the native *P. australis* strain appears restricted to small patches in urban areas and to rural areas throughout the state. In the greenhouse experiment, the nonnative strain grew taller and expanded its aboveground biomass faster than the native strain, which may give the nonnative strain a competitive advantage over the native strain in terms of light and space. Further research is needed to determine how the nonnative strain competes with the native strain and other wetland species under field conditions. Identification of native stands of *P. australis* across Utah and consideration of their presence in reed management is encouraged.

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APPENDIX. Accession numbers for herbarium samples. Brigham Young University (BYU) samples are from the S.L. Welsh Herbarium and the Utah State University (USU) samples are from the Intermountain Herbarium.

Sample	Herbarium accession number	Collection date	Haplotype
1	BYU 10883	22 Aug 1945	native
2	BYU 27256	10 Sep 1955	native
3	BYU 2433	13 Aug 1963	native
4	BYU 4356	2 Oct 1964	native
5	BYU 10796	1 Sep 1970	native
6	BYU 3136	21 Aug 1971	native
7	BYU 103367	26 Aug 1971	native
8	BYU 166384	10 Aug 1976	native
9	BYU 160432	4 Sep 1976	native
10	BYU 173326	2 Aug 1977	native
11	BYU 175465	23 Aug 1977	native
12	BYU 192127	17 Aug 1978	native
13	BYU 189356	19 Sep 1978	native
14	BYU 189424	27 Sep 1978	native
15	BYU 192221	6 Oct 1978	native
16	BYU 199474	1 Aug 1979	native
17	BYU 213010	17 Jun 1980	native
18	BYU 21887	16 Aug 1980	native
19	BYU 232641	2 Sep 1981	native
20	BYU 22539	21 Aug 1983	native
21	BYU 270575	1 Sep 1984	native
22	BYU 285668	5 Sep 1985	native
23	BYU 304378	2 Jun 1986	native
24	BYU 296613	22 Jul 1986	native
25	BYU 328245	31 Jul 1988	native
26	BYU 427604	6 Sep 1999	native
27	BYU 430042	10 Aug 2000	nonnative
28	BYU 444006	14 Aug 2000	native
29	BYU 439009	17 Aug 2000	native
30	BYU 28346	5 Oct 2001	native
31	BYU 475615	5 Oct 2005	native
32	BYU 246172	unknown	native
33	USU 18291	28 Jun 1933	native
34	USU 93681	21 Aug 1957	native
35	USU 20328	23 Aug 1934	native
36	USU 29031	12 Sep 1931	native
37	USU 108359	31 Oct 1963	native
38	USU 211221	12 Jun 1993	nonnative
39	USU 223290	14 May 1997	native