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PHRAGMITES INVASION

Life on the edge: reproductive mode and rate of invasive *Phragmites australis* patch expansion

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Abstract The dynamics of plant invasions from initial colonization through patch expansion are driven in part by mode of reproduction, i.e., sexual (seed) and asexual (clonal fragments and expansion) means. Expansion of existing patches—both rate and mode of spread into a matrix of varying conditions—is important for predicting potential invader impacts. In this study, we used fine-scale genetic assessments and remote sensing to describe both the rate and mode of expansion for 20 *Phragmites australis* patches in flooded and unflooded wetland units on the Great Salt Lake, UT. We found that the majority of *Phragmites* patch expansion occurred via clonal spread but we also documented instances of (potentially episodic) seedling recruitment. The mode of patch expansion, inferred from patch edge genet richness, was unrelated to flooding in the wetland unit in the preceding growing season. The rate of *Phragmites* patch expansion varied from 0.09 to 0.35 year^{-1} and was unrelated to the mode of spread. In six patches monitored across two years, monoclonal patches stayed monoclonal, whereas patches with higher genet richness had a marked increase in diversity in the second year. The findings of the present study suggest how this partially clonal species can exploit the benefits of both sexual (i.e., genetic recombination, widespread dispersal, colonization of new areas) and asexual reproduction (i.e., stability of established clones suited to local environmental conditions) to become one of the most successful wetland plant invaders. To control this species, both forms of reproduction need to be fully addressed through targeted management actions.

Keywords Clonality · Common reed · Genetic diversity · Genet richness · Invasive species · Seedling recruitment · Sexual reproduction

Guest Editors: Laura A. Meyerson and Kristin Saltonstall/Phragmites invasion.

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Introduction

The dynamics of clonal plant invasions from colonization through patch spread are driven by complex, interacting factors including both mode of reproduction and disturbance regime. Clonal invasive plants have the ability to spread both sexually (seeds) and asexually (i.e., without genetic recombination; Halkett et al. 2005). Seed-based reproduction in these species is generally associated with greater dispersal distances and more efficient colonization following disturbance than asexual reproduction (Grace 1993; Silvertown 2008), and can lead to increased genetic diversity and adaptive potential. However, seedlings are poorly provisioned compared to vegetative propagules (Silvertown 2008), and ramets are more robust and resilient than seedlings, particularly under suboptimal conditions, because they are subsidized by the maternal plant (Grace 1993; Honnay and Bossuyt 2005). Colonization and establishment of invasive plants is frequently initiated via seed episodically, following pulse disturbances such as removal of existing vegetation and (in wetlands) hydrologic drawdowns (Eriksson 1989), but sustained by vegetative expansion.

Spatial patterns of clonal (genotypic) diversity can reveal the relative contributions of sexual versus asexual reproduction to invasion initiation and progress, and can contribute to our understanding of disturbance histories (Eriksson 1989; Koppitz et al. 1997) During an invasion, spatial coverage of the invasive species may increase by the establishment of many new, small patches or by expansion of existing patches. While expansion of a clonal invasive species through the establishment of many new patches over time suggests ongoing seedling recruitment, the expansion of *existing* patches does not necessarily indicate the absence of seedling recruitment. Seedling recruitment can occur at patch edges due to a combination of high seed rain (with the majority of seeds likely originating from the patch itself), a facilitation effect at the patch edge, or a disturbed habitat margin. The genet richness and expansion rates at patch edges are particularly important indicators of invasion mechanisms and outcomes, but high-density sampling at patch edges is rarely investigated. In this study, we use high-density sampling along patch edges over time to make inferences about invasion dynamics in a common invasive wetland species, *Phragmites australis*.

The Eurasian lineage of *Phragmites* is a widespread, aggressive invasive species that can reproduce both sexually and asexually to invade wetlands and disturbed habitats across North America (Saltonstall 2002; Kettenring et al. 2012). Sexual reproduction and spread likely plays an important role in *Phragmites* colonization into disturbed habitats across its North American invasion (Belzile et al. 2010; McCormick et al. 2010a, b; Kirk et al. 2011; Kettenring and Mock 2012; Albert et al. 2015). Colonization of new areas by seed is likely episodic, coinciding with disturbance to matrix vegetation (Kettenring et al. 2015) and hydrologic drawdowns resulting in exposed mudflats (ter Heerdt and Drost 1994; Clevering and Lissner 1999; Alvarez et al. 2005; Wilcox 2012) because flooding greatly reduces seedling emergence and growth (Weisner et al. 1993; Armstrong et al. 1999; Mauchamp et al. 2001; Chambers et al. 2003; Baldwin et al. 2010).

Following initial colonization of an area by *Phragmites*, continued invasion may occur via ongoing establishment of new patches (i.e., colonization) or via expansion of existing patches (Lathrop et al. 2003). Expansion of existing *Phragmites* patches is expected to be largely asexual, due to rhizomes and stolons (Amsberry et al. 2000; Minchinton and Bertness 2003; Bart et al. 2006; Brisson et al. 2010; Bhattarai and Cronin 2014). This expansion would result in lower genet richness at expanding patch edges, as clones are lost to intraspecific competition over time in the absence of conditions supporting additional seedling recruitment (Koppitz and Kühl 2000; Hazelton et al. 2015). Expansion of existing patches can also occur via seedling recruitment at patch edges, particularly with drawdowns and disturbances to matrix vegetation. Patch edge expansion by seed would be expected to increase levels of genet richness at patch edges relative to patch interiors (Koppitz et al. 1997; Clevering and Lissner 1999; Koppitz 1999; Kettenring et al. 2015).

The rate of spread is also an important aspect of *Phragmites* invasion. Large and/or rapidly expanding patches will have a pronounced impact on wildlife habitat and ecosystem functions (Lathrop et al. 2003). Factors contributing to the speed of patch expansion include ongoing disturbance regimes as well as the reproductive mode at patch edges. Patch edge expansion via seedlings would enhance genetic diversity, adaptive potential, and outcrossing rates, producing a

positive feedback mechanism for further patch expansion (Baldwin et al. 2010; Kettenring et al. 2011). Polyclonal patch edges are likely to have broader ecological amplitudes because they are more likely to include clones that are well-suited to local environmental conditions (Koppitz et al. 1997; Koppitz 1999; Koppitz and Kühl 2000). Seeds colonizing patch edges may also contribute to a more rapid patch expansion than vegetative spread based simply on dispersal potential (Grace 1993; Silvertown 2008). However, seedlings may be less vigorous and have lower survival rates than rhizome or stolon shoots (Albert et al. 2015), and may not compete well initially with vegetatively spreading clones. A wide array of studies have previously estimated the rate of *Phragmites* patch expansion both in its native European range and as an invader in North America (e.g., Rice and Rooth 2000; Warren et al. 2001; Havens et al. 2003; Lathrop et al. 2003; Wilcox et al. 2003; Alvarez et al. 2005; Hudon et al. 2005; Philipp and Field 2005; Maheu-Giroux and de Blois 2007; Howard and Turluck 2013; e.g., Altartouri et al. 2014; Bhattarai and Cronin 2014). Here we present new data on spread rates in the western range of *Phragmites* invasion in North America, where its invasion is much more recent and the climate is very different from other regions of its invasion in North America where it has been intensively studied (e.g., New England, southern Quebec, Great Lakes region, Chesapeake Bay, Gulf Coast; Kettenring et al. 2012). In addition, for the first time, we relate *Phragmites* patch expansion rates with the dominant mode of reproduction.

Fine-scale assessments of genet richness over time (i.e., resolution finer than 5–10 m between samples) at the edge of *Phragmites* patches can inform our understanding of the rate and nature of patch expansion. Only one previous study has looked at invasive *Phragmites* genetic diversity at a fine spatial scale (samples 1.5–6 m apart): Douhovnikoff and Hazelton (2014) compared four native and non-native *Phragmites* patches in Maine, finding that non-native *Phragmites* had smaller clones and more frequent sexual reproduction than native *Phragmites*. These findings were similar to those in a previous study conducted with a coarser sampling scheme in native vs. non-native *Phragmites* in Utah (Kettenring and Mock 2012). However, neither Douhovnikoff and Hazelton (2014) nor Kettenring and Mock (2012) focused specifically on patch edges, where current

expansion is expected to occur. To date, the dynamics of *Phragmites* patch edges over time have not been explicitly investigated.

The objectives of our study were four-fold. Our *first objective* was to determine the relative importance of sexual versus asexual spread (using genet richness as a metric) in the expansion of 20 *Phragmites* patch edges under flooded and unflooded conditions. We hypothesized that *Phragmites* patch edges would spread predominantly by asexual means under flooded conditions, because flooding inhibits seedling emergence and growth (Weisner et al. 1993; Armstrong et al. 1999; Mauchamp et al. 2001; Chambers et al. 2003; Baldwin et al. 2010), but by seeds under unflooded conditions due to abundant *Phragmites* seed production and previously documented high rates of seedling emergence with drawdowns (ter Heerdt and Drost 1994; Clevering and Lissner 1999; Alvarez et al. 2005; Wilcox 2012). Our *second objective* was to examine the influence of initial levels of patch edge genet richness on diversity patterns in subsequent years. We predicted that with increasing genet richness at patch edges in the first year, we would see a further increase in genet richness in the second year due to the genetic diversity-viable seed production positive feedback on seedling recruitment (Kettenring et al. 2010, 2011). Our *third objective* was to evaluate the rate of spatial coverage increase in *Phragmites* over time due to patch edge expansion in the same 20 patches using a remote sensing approach. We expected that the rate of *Phragmites* patch expansion in this region would be relatively high (compared with other regions of its North American invasion) due to the sometimes unvegetated matrix and frequent hydrologic drawdowns in the study region. Our *fourth objective* was to relate the rate of *Phragmites* patch expansion to the predominant mode of reproduction at patch edges. We hypothesized that *Phragmites* patch edges with higher genet richness (an indicator of sexual reproduction) would expand more rapidly than monoclonal patch edges.

Methods

Site description

This study was conducted at the U.S. Fish and Wildlife Service's Bear River Migratory Bird

Refuge (BRMBR), which is located at the terminus of the Bear River on the northeastern edge of the Great Salt Lake. Non-native *Phragmites* first invaded Great Salt Lake wetlands (including the BRMBR) in the early 1990s, after the retreat of the lake following historic flooding for almost 6 years starting in 1983 (Olson et al. 2004; Kulmatiski et al. 2011; Kettenring et al. 2012; Vanderlinder et al. 2013). The >30,000 ha BRMBR consists of 26 wetland units, constructed following the 1980s flooding (Downard and Endter-Wada 2013). These units are managed to capture water during spring snowmelt buffering wetlands from extreme drops in water levels during the agricultural growing season, when much of the Bear River is diverted, and to maintain water levels for a diversity of priority waterbird species (Olson et al. 2004; Downard and Endter-Wada 2013; Welsh et al. 2013; Downard et al. 2014). All sampling occurred in BRMBR units 3A, 2D, 3D, and 3C (Fig. 1).

Overview

To address our study objectives, we identified 20 *Phragmites* patches to sample intensively for assessment of sexual versus asexual spread. Patches were chosen based on the following criteria: (1) were not sprayed by managers during the previous 3 years according to manager records, (2) showed no signs of herbicide damage, (3) were at least 30 m in diameter on their longest axis, (4) were within the boundaries of the flight path of an unmanned aerial vehicle (UAV) collecting remote sensing imagery for this and another study, and (5) maximized the distances between patches of the remaining patches that met criteria (1)–(4). We defined the patches in the field (as opposed to using aerial images) as a contiguous cover of robust *Phragmites*, with a well-defined margin and isolated from other *Phragmites* patches by ≥5 m (following McCormick et al. 2010b). We targeted 10 patches in units that were flooded in 2010 (3A and 2D) and 10 patches in units that were drawn down in 2010 (3C and 3D; Fig. 2) to test our hypothesis that *Phragmites* spreads predominantly by rhizomes under flooded conditions but by seeds under unflooded conditions.

Genetic analyses

Fine-scale patterns of genet richness and reproductive mode (2010)

In September 2010, in 20 *Phragmites* patches, we collected leaves every 0.5 m along each of two concentric 25.5 m transects along the patch margins (Fig. 2). The first transect, innermost to the patch ("inner transect"), followed the approximated edge of the densest part of the patch. The second transect followed the edge of the patch at approximately 50 % of maximum stem density ("middle transect"). We also sampled any "stragglers" that were on the invasion front of the patch that were at approximately <10 % of maximum stem density. For four *Phragmites* patches (3A01, 2D10, 3D11, and 3C20), all sampled leaves were genotyped to determine the optimal sampling intensity for evaluating genet (clonal) richness. Sampling occurred toward the end of the growing season in order to capture stems that would have emerged that year either by seed or rhizome (in addition to plants that may have emerged in previous years) under the current growing season's flooding regime.

Based on the sampling redundancy levels observed in these four patches, we reduced the number of samples genotyped for the 16 remaining patches. In these patches, we only analyzed samples from (1) the "stragglers" and (2) samples from every 1.5 m along the middle transect. So that all 20 patches could be comparably evaluated for genet richness, we only used a subset of the data from the four intensively sampled patches, using the samples from comparable locations (i.e., every 1.5 m) to the 16 patches.

Genet richness and reproductive mode between years (2010 vs. 2011)

In September 2011, we resampled six patches (3A01, 3A03, 3D11, 3D13, 3C18, 3C20) to evaluate changes in genet richness and mode of reproduction in the same patch between years. We used a reduced sampling scheme in 2011, sampling every 1.5 m along the middle and innermost transects, in addition to sampling the "stragglers". We attempted to lay the transects in the same locations as in 2010 although
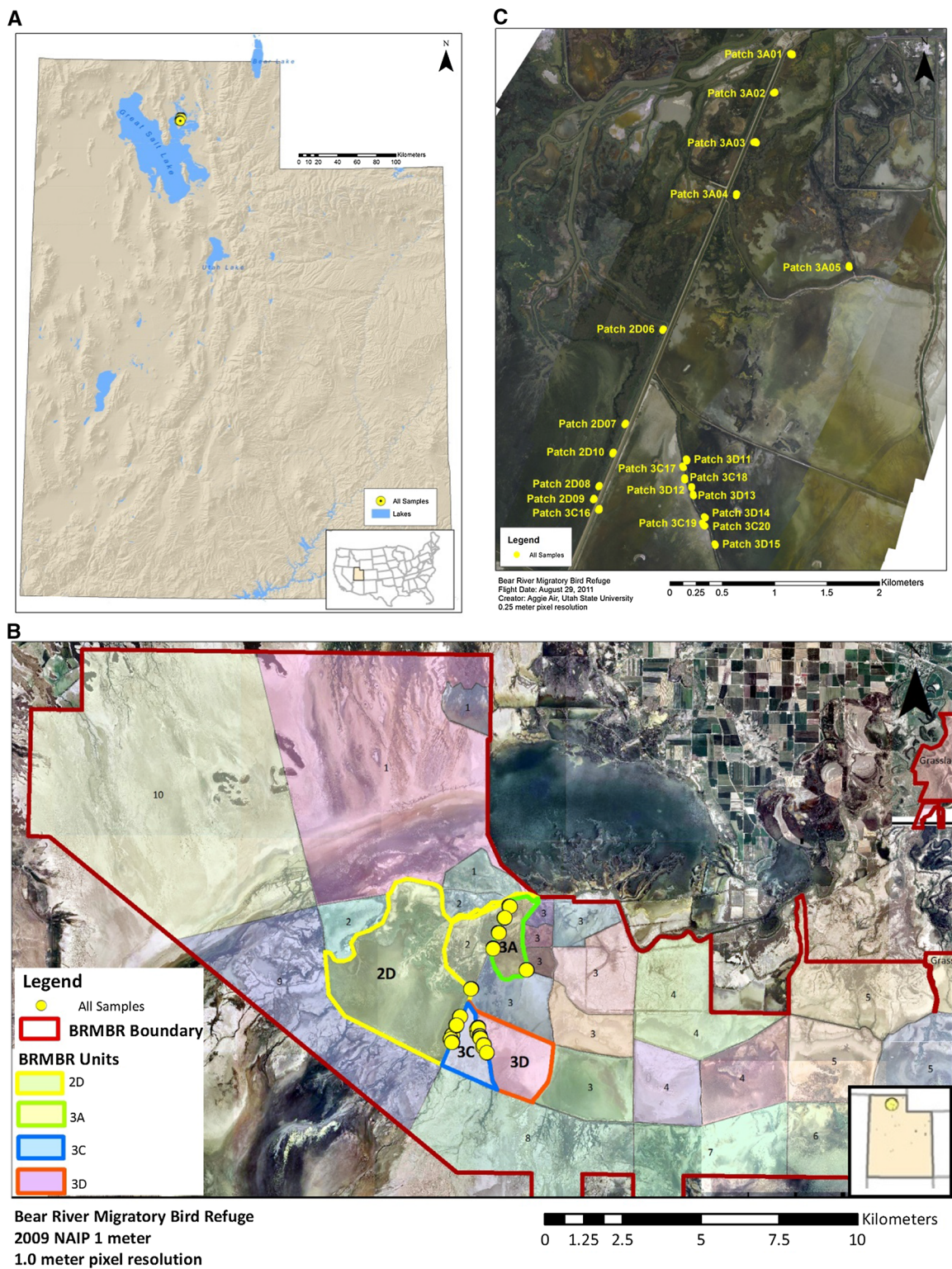
Fig. 1 The study location in (A) northern Utah within (B) a federal national wildlife refuge, the Bear River Migratory Bird Refuge in (C) four wetland units—2D, 3A, 3C, 3D

this placement was not exact due to variation in GPS accuracy and precision in the field and the challenges of conducting field work in sometimes impenetrable *Phragmites* stands. So that genet richness values were comparable with 2010 samples, we excluded 2011 data from the innermost transect in our analysis. All wetland units (and therefore *Phragmites* patches) were flooded in 2011 due to extremely high snowpack in the winter of 2010–2011. Therefore, our genet richness assessment based on presence or absence of flooding was limited to the 2010 dataset (see previous section).

Laboratory procedures

Leaf samples collected in the field were preserved by placing them in paper envelopes submerged in a silica gel desiccant and transported to the laboratory. In the laboratory, DNA was extracted from the leaf tissues using a Qiagen DNEasy 96 Plant Kit. Variation in individual DNA samples was characterized using amplified fragment length polymorphism (AFLP)

analysis (Vos et al. 1995) with modifications described by Mock et al. (2004). This technique uses a combination of restriction enzymes and polymerase chain reaction (PCR) to identify genetic differences among individuals. We used the following selective primer combinations (*5′ 6-FAM labeled): *Eco-AAC/Mse-AGC; *Eco-ACC/Mse-ACT; *Eco-ACG/Mse-ACA; *Eco-ACG/Mse-ATC; *Eco-AGG/Mse-ACT. Amplicons were separated on a sequencing gel with a LIZ500 (Applied Biosystems) size standard using an ABI 3730 automated sequencer. Individual profiles were scored for each selective primer combination using Genographer 2.1 software (Benham 2001). Markers were scored if they were polymorphic (99 % criterion). Using this technique we analyzed data from 110 variable sites (loci) in the *Phragmites* genome. This set of loci gave us ample power to discern genetically distinct individuals (genets) that arose from different seeds, and also allowed us to identify multiple stems (ramets) that arose originally from the same seed but which have spread asexually
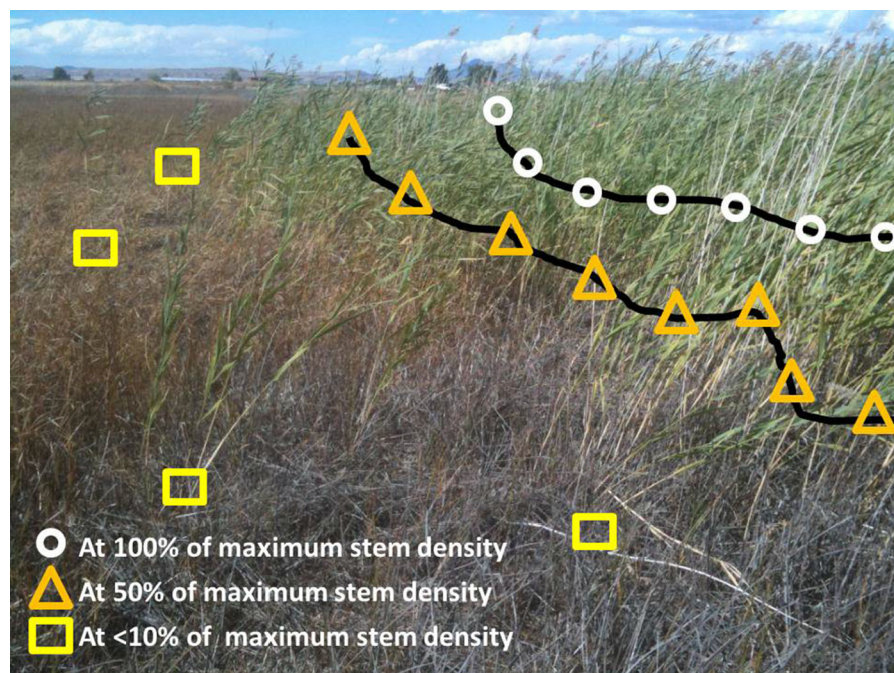
Fig. 2 Sampling scheme for *Phragmites* leaf collection for genet richness assessment in 2010 in 20 *Phragmites* patches. The inner (*white circles*; edge of 100 % maximum stem density) and middle (*orange triangles*; edge of 50 % of maximum stem density) transects were 25.5 m long and samples were initially collected every 0.5 m (although for 16 patches we only analyzed

samples every 1.5 m—see "Methods"). The yellow squares represent "stragglers"—stems that formed the invading edge of *Phragmites* patches at <10 % of maximum stem density. In 2011, in six patches, we used a similar sampling scheme except samples were collected every 1.5 m for the *inner* and *middle* transects, and in the same manner as in 2010 for the "stragglers"

through rhizomes (following Kettenring and Mock (2012), data not shown). Thus, we were able to estimate the relative spread by sexual versus asexual means in flooded versus unflooded units.

Samples were run in three phases: two in 2010 and one in 2011. Because AFLP amplification and scoring can vary across runs, we performed our scoring and genet definitions in three phases. In each phase, genets (samples from ramets originating from a single seed) were identified using the approach of Meirmans and van Tienderen (2004), where variance due to error and somatic mutations were separated from variance due to true genet differences on the basis of a strongly bimodal distribution of the number of mismatches per pair of samples. The threshold number of mismatches required to identify distinct genets (vs. error/somatic mutational differences within genets) was taken as the mismatch category between the two modes with the fewest observations. In all three phases, the two modalities were well-separated, with multiple mismatch categories between the modes which were not observed. In the first phase, a subset of the samples collected in 2010 were extracted and subject to AFLP analysis, and 110 polymorphic loci were scored. Samples with 12 or fewer mismatches were considered to be due to error/somatic mutational differences (average 0.61 mismatches per pair), while sample pairs with over 22 mismatches were considered to be different genets (average 53.08 mismatches per pair). There were no observed pairs of samples with mismatches between 13 and 22 mismatches. In the second phase, DNA extractions from genets identified in the first phase that were represented by 2 or more samples were included as references, and the AFLP analytical and scoring protocol were repeated. The second phase AFLP data (remaining 2010 samples) consisted of 117 polymorphic loci, where samples with 5 or fewer mismatches were pooled into genets (average 0.17 mismatches per pair), and samples with 6 or more mismatches were considered separate genets (average 40.27 mismatches per pair). The third phase AFLP data (from 2011 samples, including previous genet references as described above) consisted of 128 polymorphic loci, where samples with four or more mismatches were pooled into genets (average 0.06 mismatches per pair), and samples with six or more mismatches were considered separate genets (average 46.70 mismatches per pair). There were no pairs with five mismatches. In all three phases at least 10 % of the samples were replicated (from the DNA extraction step) as a quality control measure, and our mismatch rate was <1 % of individuals by loci. Pairwise genetic distances between genets were measured as the number of mismatches between the most common genotypes in each genet.

Remote sensing and vegetation classification to assess changes in *Phragmites* cover

The analysis of spread rates of the 20 *Phragmites* patches involved supervised classification of processed images obtained with UAV flights (AggieAir™) over the BRMBR on two dates (June 17, 2010 and July 21, 2011) under clear sky conditions. Imagery were collected in the red–green–blue (RGB) and near-infrared (NIR) wavelengths at a spatial resolution of 25 cm and a radiometric resolution of 8 bits. In addition, 472 ground sample locations for *Phragmites* and 37 ground sample locations for the mixed vegetation (hereafter "mixed veg") class which consisted of *Bolboschoenus maritimus*, *Schoenoplectus acutus*, *Typha* spp., wet and dry playa with and without *Salicornia* spp., along with wet meadow species such as *Carex* spp., *Distichlis spicata*, and *Eleocharis* spp. were recorded with a survey-grade GPS unit for later use in the imagery classification. A supervised multiclass relevance vector machine (MCRVM) classification algorithm (Tipping 2001; building on previous algorithms developed by Thayananthan et al. 2006) was developed for detection of location and spread of the 20 *Phragmites* patches. The MCRVM was used to classify processed and orthorectified mosaics consisting of the red, green, and near-infrared bands. The ground cover classes used in the analyses were (1) open water (hereafter "water"), (2) *Phragmites*, (3) salt/concrete (hereafter "salt"), (4) generic marsh (hereafter "marsh") consisting of low lying areas with submerged vegetation, and (5) mixed veg. Ground sample locations (northing and easting) were available for *Phragmites* and mixed vegetation. The sample locations for the other three classes were prepared from the high resolution image itself (45 for salt, 45 for marsh, and 40 for water). The inputs to the MCRVM were the reflectance values of these classes in the red, green, and near-infrared bands. The point reflectance values were extracted in GIS using location information of these five classes. Each class had a unique spectral signature which was used by the

MCRVM for building the spectral signature-class relationship.

In the training phase, the MCRVM was trained with 372 training samples of *Phragmites* spread uniformly over the wetland; 30 samples each of water, salt, and marsh; and 17 samples of mixed veg. Out of the 472 potential training samples of *Phragmites* there were around 60 samples which were not considered as "pure" samples as they were in standing water in the imagery. To avoid mixing of the spectral response of *Phragmites* and water, these 60 points were not used for training the model. From this training, the MCRVM learned an input–output relationship. The performance of the model depended heavily on the accuracy of the data and also on the size of training and test sets. For accuracy assessment of the model, confusion matrices were generated from the classification results and a Kappa statistic was calculated. The Kappa coefficient is used to measure the agreement between predicted and observed categorizations of a dataset while correcting for agreement that occurs by chance (Viera and Garrett 2005). Kappa values lie between −1 and +1. A Kappa value of zero indicates agreement by chance, a value of 1 indicates perfect agreement, and a negative value indicates potential systematic disagreement between observed and classified values (Viera and Garrett 2005). Kernel width, type of kernel, and iterations were the other parameters that controlled model performance. The kernel types that were considered were Gaussian, polynomial, spline, and radial basis kernel, of which the Gaussian kernel performed the best. In the test phase, posterior probabilities of class membership were generated and the final class was selected based on a maximum Bayesian posterior probability rule.

For testing the accuracy of the MCRVM, 100 sample points were used that had not been previously seen during the model development stage. Out of the 100 test points, 10 points for water and 15 points each for salt and marsh were randomly selected from the image using Matlab commands; 20 points for mixed veg, and 40 points for *Phragmites* were available from ground sampling. This accuracy assessment was used to calculate the producer's accuracy, user's accuracy, overall accuracy, errors of omission, and errors of commission. An error of omission occurs where a sample should have been included in a certain class, but was included in another; commission errors are when samples are included in a certain class when they

should not have been (Congalton 1991; Jensen 2005). The overall accuracy is determined by summing all of the correctly identified samples (numbers within the matrix diagonal) and dividing by the total number of samples. The producer's accuracy is a measure of the omission error and it specifies the probability of a ground reference point being correctly classified. It is calculated by dividing the diagonal number from a class's column by the sum of the entire column including the number found within the diagonal. The user's accuracy is a measure of the commission error and it indicates the probability of how well the classified sample represents what is found on the ground. It is calculated by dividing the diagonal of a class by the sum of the numbers within the row of that class (Congalton 1991; Jensen 2005).

Analysis

Genet (or clonal) richness for each patch edge was calculated as (number of genets in a patch − 1)/ (number of samples in a patch − 1) (Dorken and Eckert 2001); genet richness values can range from 0 (monoclonal patches) to 1 (all samples genetically unique). We used a *t* test to compare genet richness between patches in flooded and unflooded units (in JMP 11.0, here and below unless otherwise noted). Singletons, the number of genetically unique samples (clones) in a patch, are also reported.

In order to compare the genetic distances among clones within patches to genetic distances among clones in different patches, we constructed parallel matrices of (1) "1" versus "2" values for genets "within" and "between" patches and (2) AFLP distances (numbers of mismatches) among all genets, generated in GenAlEx (Peakall and Smouse 2006, 2012). We used a Mantel test, as implemented in the Analysis of Phylogenetics and Evolution (ape) package for R (http://ape-package.ird.fr/; mantel.test function), with the default arguments, to determine whether distances among genets within patches was significantly ($p < 0.05$) different from distances among genets in different patches. For this analysis, the five genets found in multiple patches (see below) were assigned to the patch where the majority of the samples were identified. Additionally, to determine whether the issue of genets in multiple patches impacted the Mantel results, we created and analyzed an additional dataset from which these genets were removed.

For each of the 20 *Phragmites* patches, the MVRVM classification algorithm, when applied to the imagery, was able to identify a set of contiguous pixels having a clear boundary within which all pixels were classified as "*Phragmites*" and outside of which the land cover had other classifications. The area of a patch was calculated using the patches thus identified through the MVRVM classification procedure. The changes in *Phragmites* patch cover were calculated between the two time points, both as a percent increase in whole patch area [(area in 2011 − area in 2010)/area in 2010], and as an intrinsic rate of increase for the whole patch. The intrinsic rate of increase (r) was calculated using the logarithmic growth equation $N = N_0 e^{rt}$ where N = area in 2011, N_0 = area in 2010, e = a constant (base of natural logarithm), and t = difference in years between the sampling periods (1.08 years) following Wilson and Bossert (1971). This equation was solved for $r = (\ln(N_1) - (\ln N_0))/t$. For the six patches sampled in both 2010 and 2011, we also looked at the patch expansion (area gained) between the "straggler" transects between years. For all 20 patches, we used simple linear regression to evaluate the relationship between patch edge genet richness in 2010 (an indicator of mode of reproduction) versus expansion rates (intrinsic rate of increase year^{-1}) between 2010 and 2011. We ran a similar analysis for the six resampled patches wherein we looked at the relationship between expansion between the "straggler" transects between 2010 and 2011 and genet richness in 2011 of that same patch edge, using simple linear regression.

Results

Fine-scale patterns of genet richness and reproductive mode (2010)

Out of the 470 samples analyzed in the four intensively sampled patches in 2010, we detected 16 unique genets (Table 1), based on 128 polymorphic AFLP loci. Three of the patches (3A01, 2D10, 3C20) were comprised of very few genets (1–4). One of the patches (3D11) had a relatively high number of genets (10) and singletons (6; single observation genotypes) (Table 1; Fig. 3B). The singletons in 3D11 were clustered together spatially along the leading edge of the *Phragmites* patch (Fig. 3B). There were also two very large clones that occurred throughout the patch (Fig. 3B). In patch 2D10, the other of these four patches with >1 genet, we found that the genets were generally cohesive, with two genets each spanning a large area of the patch (Fig. 4E).

Out of the 765 samples analyzed from all 20 patches in 2010, we detected 69 unique genets (Table 2). Genet richness varied widely among the patches (0.00–0.24; Table 2) and there were variable patterns of asexual and sexual spread across the 20 patches (Figs. 3, 4, 5, 6). There was no relationship between water level (flooded vs. unflooded) and genet richness at patch edges (t = 2.10, p = 0.35; Table 2).

For the four patches with the highest levels of genet richness (defined here as ≥0.15, patches 2D07, 3D13, 3C16, 3D11), we saw two emerging patterns. Some patches had genets that were generally spatially cohesive and segregated from other genets, with no single genet dominating the patch and few singletons (3D13, 2D07, 3C16; Figs. 3H, 4B, 5A). On the other hand, 3D11 appeared to have most of the different genets and numerous singletons isolated in one area within the patch while just two genets were found spread across the patch (Fig. 3B). Four of the 20 patches were monoclonal, and three of those patches were contained within the same wetland unit 3A (3C20, 3A01, 3A03, 3A05; Table 2; Figs. 5H, 6B, E, I).

There were five instances where we found identical genets in two different patches (Table 3). In three of these cases, the patches were neighboring each other within the same wetland unit. In two of the cases, the patches were in different wetland units (2D and 3A; 2D and 3D) a few hundred meters apart.

Table 1 Summary of genet data for the four patches that were intensively sampled in 2010

Patch	Water level treatment	# Samples	# Genets	# Singletons	Genet richness
3A01	Flooded	119	1	0	0.00
2D10	Flooded	119	4	1	0.03
3D11	Unflooded	120	10	6	0.08
3C20	Unflooded	112	1	0	0.00
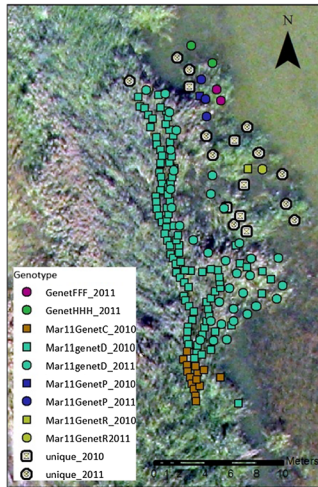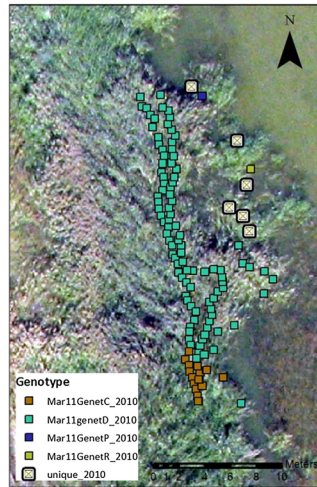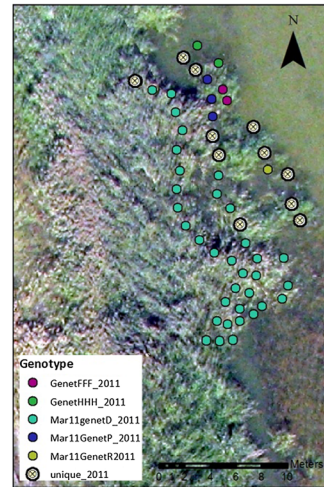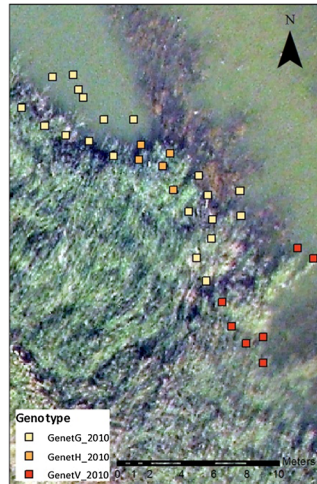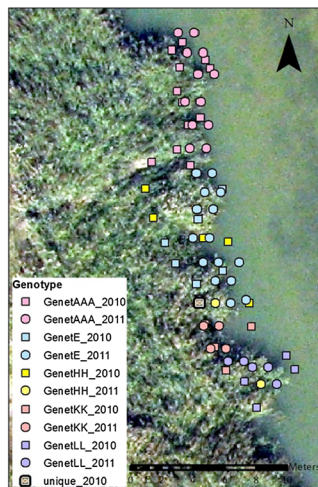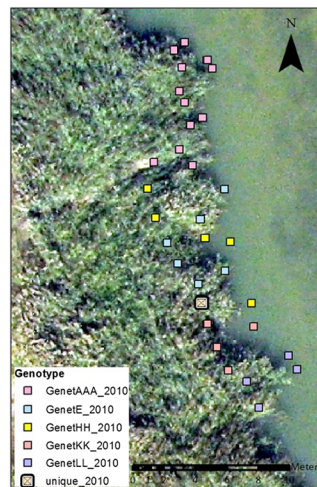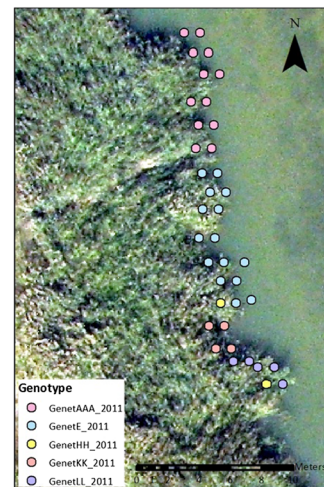
◄ **Fig. 3** The distribution of different clones within five *Phragmites* patches in Unit 3D at Bear River Migratory Bird Refuge. Samples that were genetically identical share a common *color*. Samples from 2010 that were genetically unique are denoted with an "×" in a *square* and those from 2011 are denoted with an "×" in a *circle*

Genetic distances between pairs of genets were significantly greater when genets were in different patches (mean distance 47.46) than when genets were within the same patch (mean distance 41.36, Mantel $p < 0.001$). Removal of the five genets found in multiple patches (Table 3) did not change the Mantel test results.

Genet richness and reproductive mode
between years (2010 vs. 2011)

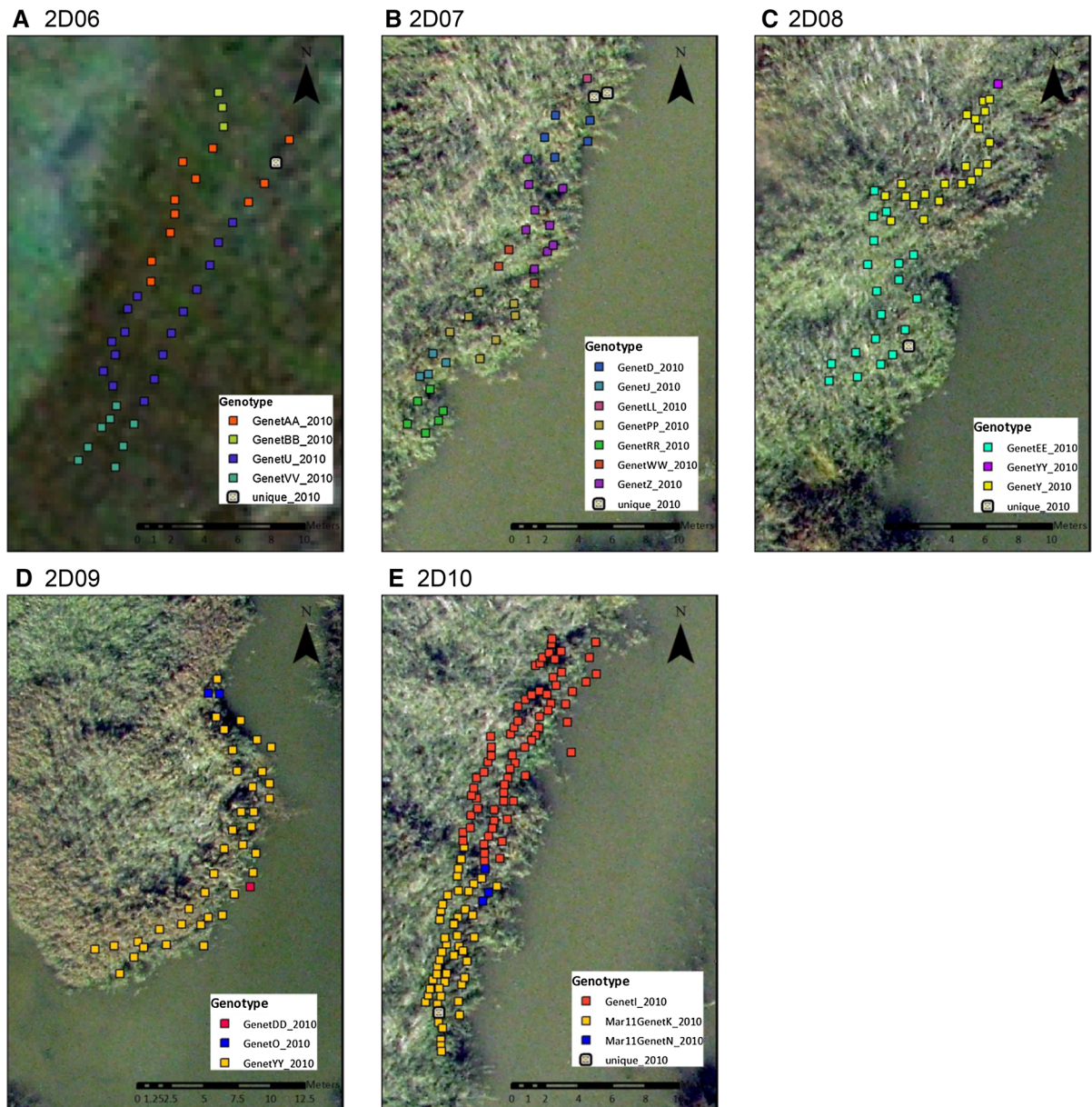When we compared genet richness within the same patch between 2 years, we found no change

Fig. 4 The distribution of different clones within five *Phragmites* patches in Unit 2D at Bear River Migratory Bird Refuge. Samples that were genetically identical share a common *color*. Samples that were genetically unique are denoted with an "×" in a *square*

in the monoclonal patches (3A01, 3A03) and low genet richness patches (3C18, 3C20), a moderate increase in genet richness for the patch with moderately high levels of genet richness (3D13), and a large increase in genet richness for the most diverse patch, 3D11 (Table 2; Fig. 3B vs. C, H vs. I, 5E vs. F, H vs. I, 6B vs. C, E vs. F). The composition of the clones was quite stable in these patches over our study period as genotypes
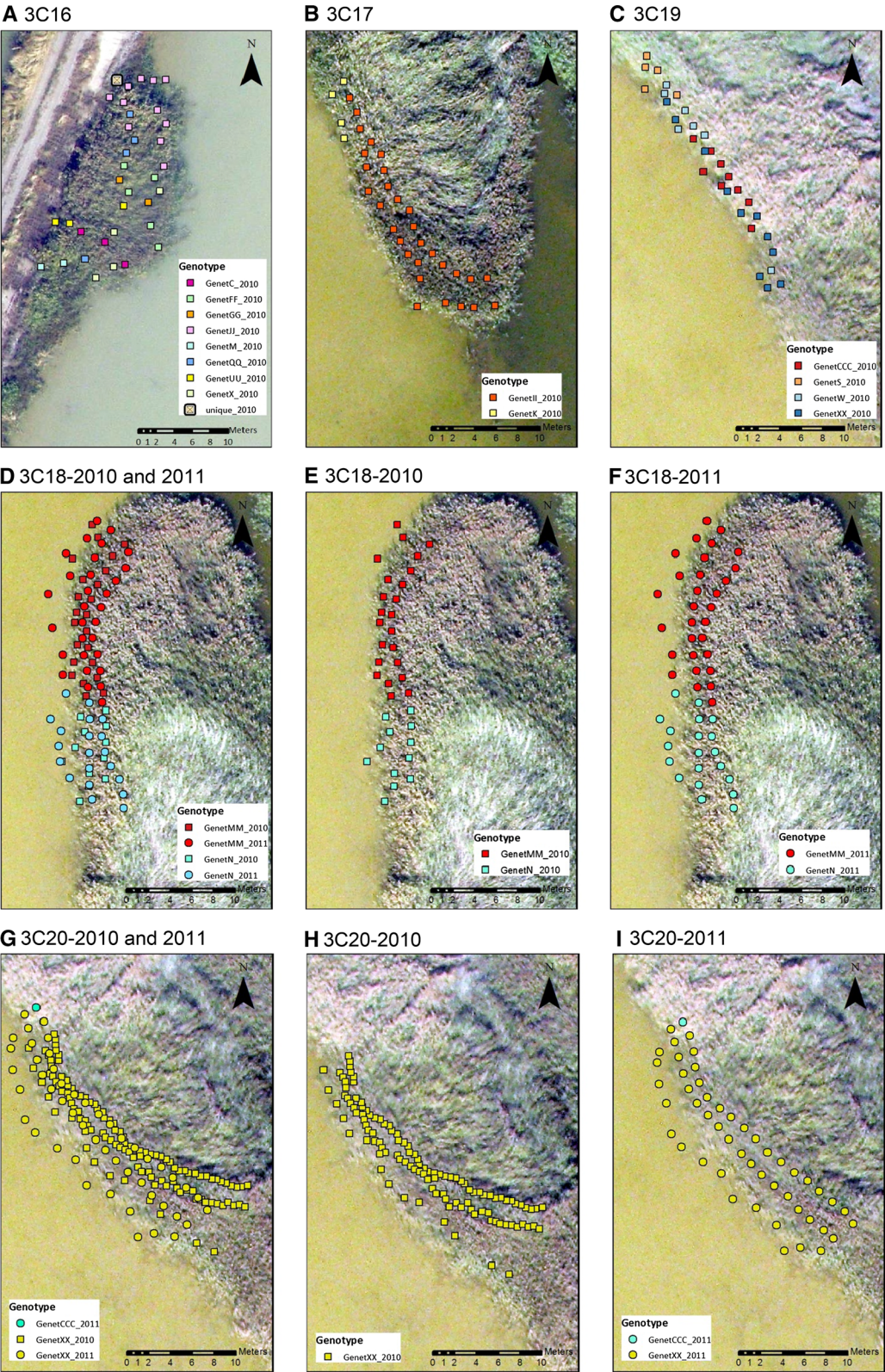
Fig. 5 The distribution of different clones within five *Phragmites* patches in Unit 3C at Bear River Migratory Bird Refuge. Samples that were genetically identical share a common *color*. Samples that were genetically unique are denoted with an "×" in a *square*

identified in 2010 were almost always recaptured in 2011 (Fig. 3H vs. I, 5E vs. F, H vs. I, 6B vs. C, E vs. F).

Table 2 Summary of genet data for all 20 patches. For 2010 data for 3A01, 2D10, 3D11, and 3C20, we excluded samples to mimic the same sampling scheme of the other 16 patches (therefore, some genets visible in the maps are not tallied below). For the six patches that we sampled in both 2010 and 2011 (3A01, 3A03, 3D11, 3D13, 3C18, and 3C20), we present both sets for comparison purposes, with 2011 sampled patches denoted with "-2011" in their patch name and again, we excluded some 2011 genet data visible in the maps to be comparable with the 2010 reduced sampling intensity

Patch	Water level	# Samples	# Genets	# Singletons	Genet richness
3A01	Flooded	39	1	0	0.00
3A01-2011	Flooded	40	1	0	0.00
3A02	Flooded	40	2	0	0.03
3A03	Flooded	45	1	0	0.00
3A03-2011	Flooded	35	1	0	0.00
3A04	Flooded	41	3	0	0.05
3A05	Flooded	47	1	0	0.00
2D06	Flooded	40	5	1	0.10
2D07	Flooded	37	9	2	0.22
2D08	Flooded	42	4	1	0.07
2D09	Flooded	40	3	0	0.05
2D10	Flooded	41	3	0	0.05
3D11	Unflooded	39	10	6	0.24
3D11-2011	Flooded	35	15	10	0.41
3D12	Unflooded	44	2	0	0.02
3D13	Unflooded	32	6	1	0.16
3D13-2011	Flooded	20	5	0	0.21
3D14	Unflooded	32	3	0	0.06
3D15	Unflooded	38	2	0	0.03
3C16	Unflooded	35	9	1	0.24
3C17	Unflooded	34	2	0	0.03
3C18	Unflooded	35	2	0	0.03
3C18-2011	Flooded	32	2	0	0.03
3C19	Unflooded	32	4	0	0.10
3C20	Unflooded	32	1	0	0.00
3C20-2011	Flooded	32	1	0	0.00
	Total (2010)	**765**	**69**[a]		**0.09**
	Flooded (2010)	**412**	**31**[a]		**0.07**
	Unflooded (2010)	**353**	**39**[a]		**0.11**
	Six patches (2010)	**222**	**21**		**0.09**
	Six patches (2011)	**194**	**25**[a]		**0.12**

[a] These totals are corrected for the repeated genets found in two patches (Table 3)
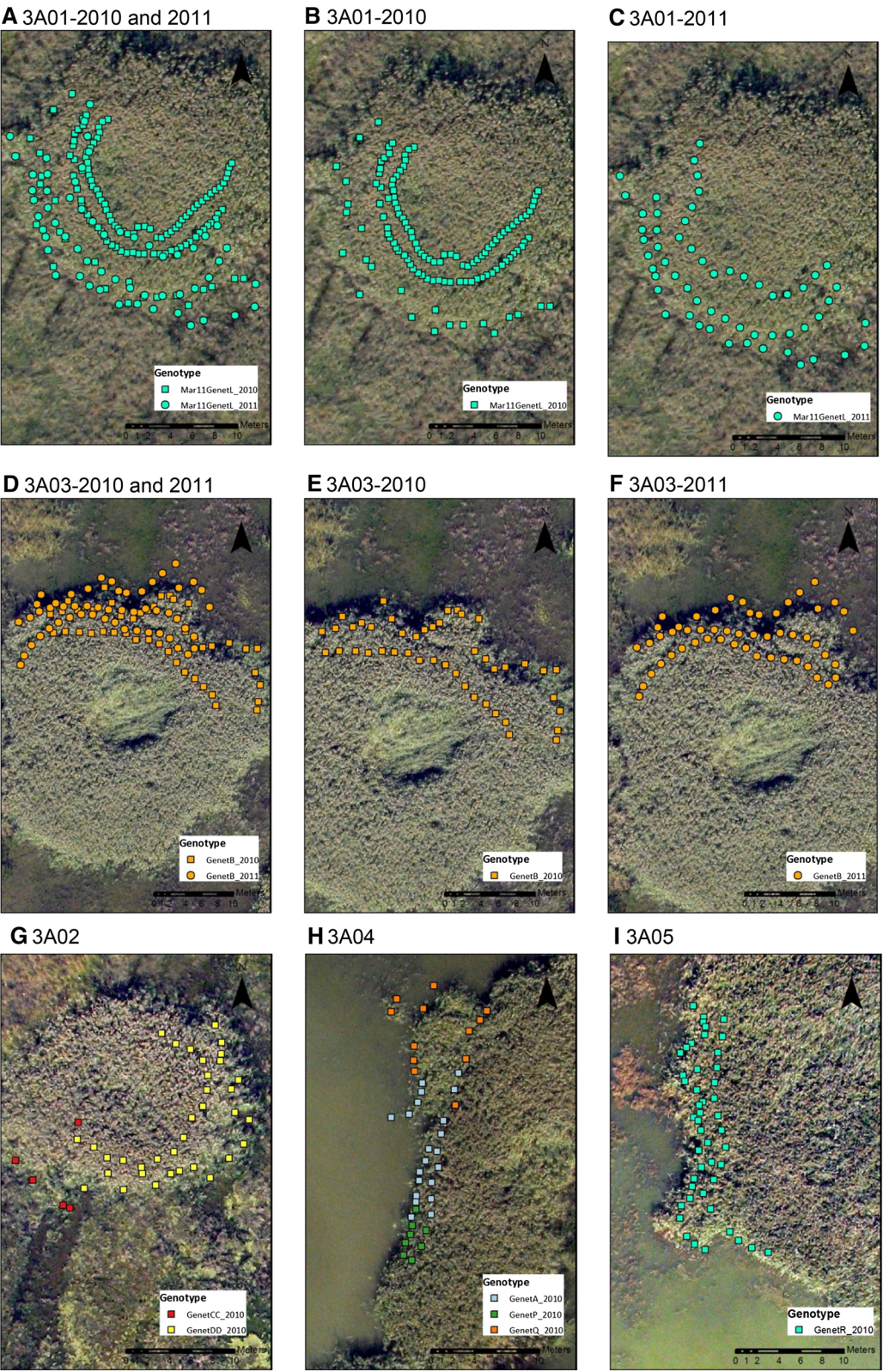
◄ **Fig. 6** The distribution of different clones within five *Phragmites* patches in Unit 3A at Bear River Migratory Bird Refuge. Samples that were genetically identical share a common *color*

Changes in *Phragmites* cover and relationship to genet richness

The overall classification accuracy for June 17, 2010 imagery was 92 % and for July 21, 2011 was 95 % (Supplementary Table 1). The *Phragmites* user's accuracy was 95 and 95 %, and the producer's accuracy was 90 and 95 %, for 2010 and 2011, respectively. These results indicated that the MCRVM model yielded a classification of high accuracy (Foody

2008). The errors of omission and commission were 10 and 5 %, respectively, for *Phragmites* in 2010 and 5 and 5 % in 2011 (Supplementary Table 2). The Kappa values for classification of June 17, 2010 and July 21, 2011 images are 0.89 and 0.93, respectively, which indicated a very good agreement between the real classes and classes mapped by the model (Viera and Garrett 2005).

Phragmites cover changed as little as 11 % per year (intrinsic rate of increase 0.09 year^{-1}; patch 3D15) and as much as 46 % per year (intrinsic rate of increase 0.35 year^{-1}; patches 3A03 and 3C16) between 2010 and 2011 (Table 4). The rate of change in whole patch *Phragmites* cover was unrelated to genet richness of

Table 3 Genets found in two *Phragmites* patches. Most genets were restricted to one patch. No genets were found in >2 patches

Genet name	Patch (# occurrences)	Patch (# occurrences)
DD	2D09 (1)	3A02 (35)
XX	3C19 (11)	3C20 (112); 3C20-2011 (49)
LL	2D07 (1)	3D13 (4); 3D13-2011 (5)
YY	2D08 (1)	2D09 (37)
CCC	3C20-2011 (1)	3C19 (9)

Table 4 Changes in cover between 2010 and 2011 for the twenty *Phragmites* patches

Patch	*Phragmites* cover in 2010 (m^2)	*Phragmites* cover in 2011 (m^2)	Patch expansion rate (% increase)	Intrinsic rate of increase year^{-1}
3A01	402	511	27	0.22
3A02	334	373	12	0.10
3A03	726	1058	46	0.35
3A04	571	710	24	0.20
3A05	359	493	37	0.29
2D06	284	377	33	0.26
2D07	565	785	39	0.30
2D08	1740	2250	29	0.24
2D09	1777	2254	27	0.22
2D10	791	983	24	0.20
3D11	505	585	16	0.13
3D12	355	437	23	0.19
3D13	343	405	18	0.15
3D14	273	368	35	0.28
3D15	510	565	11	0.09
3C16	195	285	46	0.35
3C17	537	623	16	0.14
3C18	1327	1612	21	0.18
3C19	918	1135	24	0.20
3C20	463	607	31	0.25

the patch edge ($R^2 = 0.01$; $p = 0.19$). Similarly, the expansion rate between the "straggler" transect in 2010–2011 was unrelated to genet richness of that same transect in 2010 ($R^2 = 0.12$; $p = 0.49$).

Discussion

Although there is now abundant evidence for the importance of sexual reproduction in the colonization of new areas and rapid, widespread dispersal of *Phragmites* across North America, here we present for the first time a detailed genetic assessment that informs the mechanisms of patch expansion. Understanding the mechanisms of patch expansion is critical to inform potential impacts of existing *Phragmites* patches as well as management efforts. We show that the majority of patch expansion in these Great Salt Lake wetlands occurs via clonal spread but we also document instances of (potentially episodic) seedling recruitment. These findings suggest how this partially clonally species can exploit the benefits of both sexual reproduction (i.e., genetic recombination, widespread dispersal, colonization of new areas) and asexual reproduction (i.e., stability of established clones suited to local environmental conditions) to become one of the most successful invasive plants in North America.

Patterns of genet richness and mode of reproduction

Koppitz ([1999](#)) suggested that *Phragmites* clones can be spatially isolated or can be intermingled. We found support for both scenarios in the present study in the highly variable clonal patterns across the 20 patches sampled in 2010. In many cases, we found that the genets were generally cohesive (e.g., 3A04, 3C18, 3D12) or that a patch was simply monoclonal (e.g., 3A01, 3A03), suggesting that clonal expansion was important following the establishment of a new genet by seed or clonal fragment. In other patches (e.g., 3C19, 3D14), we found that some genets were more intermingled and that the same genet could be scattered throughout a patch. This latter pattern could result from asexual spread by rhizome fragments, long extension of rhizomes, or fragmentation of one genet by expansion of others.

Of the four patches with the highest levels of genet richness (≥ 0.15), only one patch (3D11) had numerous singletons, providing the strongest evidence for a case of recent seedling recruitment contributing to patch expansion. This patch was also the only one of the six patches compared between years that showed a substantial change in genet richness over time, due again to this putative episode of seedling recruitment.

Genetic distances between pairs of genets were significantly greater when genets were in different patches than when genets were within the same patch. This pattern may be due to limited seed dispersal and/or an overabundance of pollen from within patches, either of which could cause sibling or half-sibling spatial clusters around parental clones. We were unable to assess relatedness or parentage reliably with AFLP analysis, since it is a dominant marker system.

Drivers of mode of reproduction for patch expansion

The expansion of *Phragmites* patches is controlled by multiple biotic and abiotic factors operating at different spatial and temporal scales. New patches can be established by clonal fragment or seed, and may initially be composed of a single or multiple genets. Expansion of a newly formed patch into the surrounding matrix may also occur clonally or by seed. The composition of the surrounding matrix is a strong determinant of seedling recruitment, with seedling success increasing with disturbance to matrix vegetation, hydrologic drawdowns, and other favorable abiotic conditions (e.g., suitable salinity levels) (Weisner et al. [1993](#); ter Heerdt and Drost [1994](#); Armstrong et al. [1999](#); Clevering and Lissner [1999](#); Mauchamp et al. [2001](#); Chambers et al. [2003](#); Alvarez et al. [2005](#); Baldwin et al. [2010](#); Wilcox [2012](#); Kettenring et al. [2015](#)). Patch expansion through rhizome extension would be expected to occur under a broader range of environmental conditions than seedling establishment, including flooding, since ramets of the same genet would be subsidized through a network of rhizome connections (Brisson et al. [2010](#); Bhattarai and Cronin [2014](#)).

Contrary to our expectations, the presence of flooding during the 2010 growing season did not have a strong impact on patch margin genet richness measured at the end of the 2010 growing season. This result could be due to other factors which vary and have stronger influences on patch expansion mode (e.g. disturbance to the matrix vegetation), or that a

more integrative measure of hydrologic influences across multiple growing seasons was warranted; unfortunately such disturbance and hydrological data do not exist for this study area. Our findings demonstrate the utility of fine-scale genetic assessments for uncovering patterns of genet richness and mode of reproduction in patch expansion, but such a retrospective approach does limit our ability to attribute causative factors. To delve more deeply into drivers of mode of reproduction, future work should take a prospective approach by tracking genet richness as an indicator of mode of reproduction, along with detailed monitoring of factors likely to affect mode of reproduction, over multiple years at appropriate temporal and spatial scales.

Does diversity beget diversity and drive population evolution?

Polyclonal *Phragmites* patches in Chesapeake Bay brackish wetlands have higher viable seed production and experimentally cross-pollinated plants have higher viable seed production than self-pollinated ones (Kettenring et al. 2010, 2011). Based on these results, we predicted that more genetically diverse *Phragmites* patch edges in 2010 would have a larger increase in genet richness in 2011 compared to low genet richness patch edges. Our results for the six patches compared between years align with our predictions. The two monoclonal patches (3A01, 3A03) in 2010 remained monoclonal in 2011 (Table 2). The patch with the highest genet richness in 2010 (3D11) showed the largest increase in genet richness of the six patches (0.24–0.41). Similarly, the polyclonal patches with low levels of genet richness had no change between years (3C18, 3C20), whereas the polyclonal patch 3D13 with moderate genet richness in 2010 had a small increase in 2011 (0.16–0.21). Given that we were only able to compare six patches between years (given the budgetary constraints of processing hundreds of genetic samples), we were surprised at how well our predictions matched the actual genet richness changes we observed. Alternatively, it is possible that abiotic conditions in and around the more clonally diverse patches have been, and continue to be, more amenable to seedling establishment than other patches, making it difficult to distinguish the impact of local environmental conditions versus the impact of cross-

pollination. A more robust assessment of numerous patches between years is warranted to confirm these patterns.

Monoclonal plant patches and patch edges can have failed seed reproduction, which has long term consequences for additional colonization and evolution (Honnay and Bossuyt 2005). In the present study, out of the 20 patches evaluated, four patches (3A01, 3A03, 3A05, 3C20) were monoclonal. When considering the larger landscape of *Phragmites* invasion in the region, these (and other monoclonal) patches will likely have little influence on the rapid evolution of this species as it spreads into new areas and potentially new environments, whereas patches such as 3D11 are likely strong drivers of population evolution. An added benefit of tracking existing (and newly emerging) patches over longer time frames than was possible in the present study, would be gaining new insights into the differential contributions of patches with varying genet richness to population evolution (Kettenring et al. 2011), as has been documented for another wetland invader, *Spartina alterniflora* (Daehler and Strong 1994; Daehler 1998).

Phragmites rate of expansion and potential drivers

The invasion of *Phragmites* in North America has been very well studied along the Atlantic, Gulf, and Great Lakes coasts of North America and the St. Lawrence River watershed in Canada (reviewed in Kettenring et al. 2012). The invasion of *Phragmites* into the arid western United States is more recent and largely unstudied (Meyerson et al. 2010; Kulmatiski et al. 2011; Kettenring et al. 2012; Kettenring and Mock 2012). Given the drastically different environmental conditions in this landscape (e.g., low summer precipitation, frequent drought conditions, and extreme high summer temperatures) compared with the regions mentioned above, we might have expected that *Phragmites* expansion rates would be much slower compared to other regions of North America. On the other hand, following the 1990s retreat of the Great Salt Lake after historic flooding in the 1980s, many wetlands were left completely unvegetated, with high salinity conditions, and increasingly eutrophied conditions from nearby development along the urbanizing Wasatch Front (Vanderlinder et al. 2013). Such highly disturbed conditions (particularly the high light levels preferred by *Phragmites* seeds and seedlings;

Kettenring et al. 2015) likely favored rapid *Phragmites* spread rates in areas still recovering from the flooding (Kettenring et al. 2012). As the salinity declined with freshwater flushing (precipitation and rivers that enter Great Salt Lake) to levels tolerable by *Phragmites*, this species proliferated whereas some of the native emergent species were likely inhibited by the high salinity levels and/or had slower recovery rates compared to *Phragmites*. Interestingly, when we compared the spread rates we found in the present study with a number of studies in the native (European) and introduced (North American) ranges of *Phragmites* (Table 5), we found that the intrinsic rate of increase of *Phragmites* patches was very average in Utah—both in terms of the slowest and fastest rates of patch increase. A prospective assessment of patch spread rates with simultaneous fine-scale documentation of water levels, environmental conditions potentially driving sexual and asexual spread, and the composition of matrix vegetation including its disturbance, would provide greater insight into drivers of patch expansion.

We predicted that *Phragmites* patch expansion rates would be faster in patches with higher levels of genet richness at patch edges (i.e., those likely to be established by and producing more seeds) due to the broader dispersal ability of seeds versus clonal expansion. However, we found no relationship with whole patch spread rates versus genet richness along the 25.5 m transects. Given the mismatch in spatial scale between whole patch spread and the 25.5 m transects where genet richness was assessed, we also conducted an assessment on genet richness versus the increase in area between the outermost transects in 2010 versus 2011 for the six patches for which we had such field data. Again, we found no relationship between patch expansion and genet richness. These findings suggest that other factors are likely a stronger driving force in patch expansion rates, mostly likely the condition of the matrix surrounding these patches (presence of disturbance, type of vegetation, water levels) which warrant additional evaluation.

Benefits of this fine scale genetic sampling strategy

Given the logistical and financial constraints to such a fine-scale genetic sampling strategy as was used in the

Table 5 The intrinsic rate of increase (lowest and highest value reported) of *Phragmites* per year in European and North American studies

Habitat	Location	Intrinsic rate of increase year^{-1}	References
Fresh and brackish tidal wetlands	Connecticut River estuary, USA	n/a–0.12	Warren et al. (2001)
Shoreline of Baltic Sea	Finland	0.00–0.13	Altartouri et al. (2014)
Mediterranean marsh	France	0.00–0.17	Alvarez et al. (2005)
Fresh and brackish tidal marshes	Upper Chesapeake Bay, USA	0.00–0.21	Rice and Rooth (2000)
St. Lawrence River	Quebec, CA	0.05–0.21	Hudon et al. (2005)
Brackish tidal wetlands	DE, NJ, NY, USA	0.00–0.25	Lathrop et al. (2003)
Freshwater and brackish marshes	Gulf and Atlantic coast, USA	0.06–0.35	Bhattarai and Cronin (2014)
Freshwater—brackish wetlands	Great Salt Lake, UT, USA	0.09–0.35	This study
Salt marsh	DE, USA	0.01–0.41	Philipp and Field (2005)
Constructed mitigation wetlands	VA, USA	−0.27–0.49	Havens et al. (2003)
Periurban linear wetlands	Southern Quebec, CA	0.19–0.54	Maheu-Giroux and de Blois (2007)
Coastal wetlands of Great Lakes	Lake Erie, Ontario, CA	−0.74–0.76	Wilcox et al. (2003)
Restored marsh	LA, USA	0.13–1.22	Howard and Turluck (2013)

Results are sorted by the highest rates found in each location

present study, it is not surprising that few previous studies on genetic diversity in *Phragmites* incorporated such methods. Importantly, both the findings of this study and that of Douhovnikoff and Hazelton (2014) can suggest the optimal sampling strategy for uncovering genet richness patterns without oversampling. In our study, samples taken every 1.5 m often revealed identical genets even in polyclonal patches (e.g., patch 3D13). However, more diverse polyclonal patches, such as 3D11, with sampling every 0.5 m revealed new genets. These results suggest that to fully describe genet richness in *Phragmites*, sampling every 0.5 m may be warranted. In the study of invasive (and native) *Phragmites* in Maine, Douhovnikoff and Hazelton (2014) initially evaluated whole-patch genet richness in a single invasive patch at the corners of a 1.5 m × 6 m sampling grid, and using initial results, they then assessed three additional invasive patches with a 5 m × 5 m grid repeated over the whole patch. This coarser approach is more feasible for evaluating whole patch genet richness, whereas when attempting to describe patch edge dynamics, the finer sampling scheme we employed is recommended.

Conclusions and management implications

We have shown that, through the use of fine-scale genetic assessments, we can determine the reproductive mode of *Phragmites* patch expansion. The majority of patch expansion appears to be clonally-driven although we also document cases of past and on-going seedling recruitment. Sexual reproduction is clearly important for the rapid, widespread dispersal of *Phragmites* across its invading range in North America and combined with asexual colonization and spread, *Phragmites* can invade an even broader habitat niche. Interestingly, there are an increasing number of examples of partially clonal invasive plants that utilize this strategy of dispersal largely by seed and then both sexual and clonal expansion including *Fallopia japonica* (Japanese knotweed; Grimsby et al. 2007), *Pueraria lobata* (kudzu; Pappert et al. 2000), and *Solidago canadensis* (Canada goldenrod; Dong et al. 2006). Can these emerging patterns guide more effective management of partially clonal invasive plants?

Recent revelations about the importance of genetic diversity, cross pollination, and seed reproduction in *Phragmites* invasion resulted in calls to address seed reproduction as part of a comprehensive *Phragmites* management program (Kettenring et al. 2011; Hazelton et al. 2014). However, given that *Phragmites* can capitalize on both modes of reproduction for rapid expansion and long-term stability, it is important to address all aspects of its reproductive dynamics in management. Kettenring et al. (2011) suggested that treatments such as mowing or herbicide application implemented earlier in the growing season could prevent seed reproduction. These efforts can be successful if timed to allow sufficient stand recovery for a fall herbicide application that will more effectively promote rhizome mortality and affect long-term stand persistence. Such a species biology-informed approach may be the best solution for dealing with the multiple modes of reproduction of partially clonal invaders.

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