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Clonal growth: Invasion or stability? A comparative study of clonal architecture and diversity in native and introduced lineages of Phragmites australis (Poaceae)

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BRIEF COMMUNICATION

Clonal growth: Invasion or stability? A comparative study of clonal architecture and diversity in native and introduced lineages of *Phragmites australis* (Poaceae)[1]

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- *Premise of the study:* The characteristics of clonal growth that are advantageous in invasive plants can also result in native plants' ability to resist invasion. In Maine, we compared the clonal architecture and diversity of an invasive lineage (introduced *Phragmites*) and a noninvasive lineage (native *Phragmites*) present in much of North America. This study is the first on stand-scale diversity using a sample size and systematic spatial-sampling scheme adequate for characterizing clonal structure in *Phragmites*. Our questions included: (1) Does the structure and extent of clonal growth suggest that the potential for clonal growth contributes to the invasiveness of the introduced lineage? (2) Is clonal growth common in the native lineage, acting as a possible source of ecological resistance and resilience?
- *Methods:* Microsatellite markers were used to measure clonal sizes, architecture, and diversity within each lineage in stands within four marshes in Maine.
- *Key results:* Clonal diversity measures indicated that clonal growth was significantly greater in stands of the native lineage than in the introduced. While lineage was a consistent predictor of clonal diversity relative ranking, the marsh location was a much stronger predictor of the absolute range of these values.
- *Conclusions:* Our results indicate an important role for clonal growth in the space consolidation of native *Phragmites* and could explain why the introduced lineage, with stronger competitive traits, has not replaced the native where they co-occur. These results with regard to clone size, size distributions, singleton occurrence, and clonal architecture provide some evidence for stand development that follows a genotypic initial floristics model.

Key words: clonal growth; clonal structure; introduced; invasive; native; *Phragmites*; Poaceae; resilience; resistance; stand development.

The capacity for clonal growth is often given as an explanation for the invasive character of many introduced species (Lin et al., 2009; Kui et al., 2013). Clonal growth is a form of asexual reproduction in plants involving the generation of genetically identical but potentially independent ramets. This growth affords the species a capacity for reproducing and avoiding inbreeding depression despite small initial population sizes. It also offers competitive advantages such as the ability to nurse new ramets, opportunities of scale and division of labor through resource sharing between ramets, pre-emption of resources through spatial spreading, as well as avoidance of the costs and risks involved in sexual reproduction (Alpert and Simms, 2002).

Many of the characteristics of clonal growth that are advantageous in invasive plants can also result in great stability of plants to resist invasion or other forms of change and disturbance. In fact, clonal plants have demonstrated extreme longevity, reaching thousands of years for some clonal shrubs and in excess of 10 000 yr for some trees (De Witte and Stocklin, 2010). Single ramets living up to 2000 yr in clones of coast redwood (*Sequoia sempervirens*) and genets of aspen (*Populus tremuloides*) that are measured in hectares are dramatic examples of clonal growth potential (Douhovnikoff et al., 2004; Mock et al., 2008).

Historically, *Phragmites australis* Trin. Ex. Steud. was a minor component of the native North American flora. However, over the past 4–5 decades, the clonal grass has aggressively expanded its range (Chambers et al., 1999). Saltonstall (2002) recognized that the recent invasiveness was the result of the introduction of a European lineage to the North American continent. Introduced *P. australis* subsp. *australis* rapidly colonizes new sites and forms dense monocultures, while the native *P. australis* subsp. *americanus* lineage is associated with a community of understory plants and is not an aggressive colonizer (henceforth introduced and native *P. australis*, respectively). The success of introduced *P. australis* as an invader is often credited to clonal growth and integration by mediating environmental stress and sharing resources between ramets (Amsberry et al., 2000; Bart et al., 2006). The role of clonal growth in the native is unknown and unstudied. Native and introduced *P. australis* inhabit similar environments, and in some

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instances, the introduced is suspected of outcompeting and replacing the native (Saltonstall, 2002, 2003; Meadows, 2006); however, there is no evidence of competitive advantage in New England, and in fact, the native appears to be somewhat resistant to invasion (Taddeo and deBlois, 2012).

By determining the structure of *P. australis* genotypes within stands, we can study the role of sexual and asexual reproduction in stand and population development (Douhovnikoff et al., 2005). While a small number of studies have explored genet distribution of *P. australis* at the watershed and stand scale (Keller, 2000; Křiváčková-Suchá et al., 2007; McCormick et al., 2010; Guo et al., 2013), no stand-scale studies have used a large sample size and a systematic, two-dimensional spatial sampling scheme capable of defining clonal structure. Also, work that has been done has focused on European lineages, and little is known about how their reproductive pattern might differ from that of the North American native *P. australis* (Kettenring and Mock, 2012). If capacity for clonal growth contributes to the invasive distinction between the native and introduced lineage, we hypothesize a greater role for clonality in the former.

Our study addresses the following questions: (1) Does the structure and extent of clonal growth suggest that the potential for clonal growth contributes to the invasiveness of the introduced lineage? (2) Is clonal growth a possible source of ecological resistance and resilience in the native?

Using microsatellite markers, we measured clonal structure in *P. australis* in four salt marshes in coastal Maine in the United States (Fig. 1). We systematically mapped the arrangement of individual genotypes at the stand scale and compared clonal architecture across lineages. This study is one of the first to use a systematic sampling regime to compare clonal diversity and architecture of the native and introduced conspecifics.

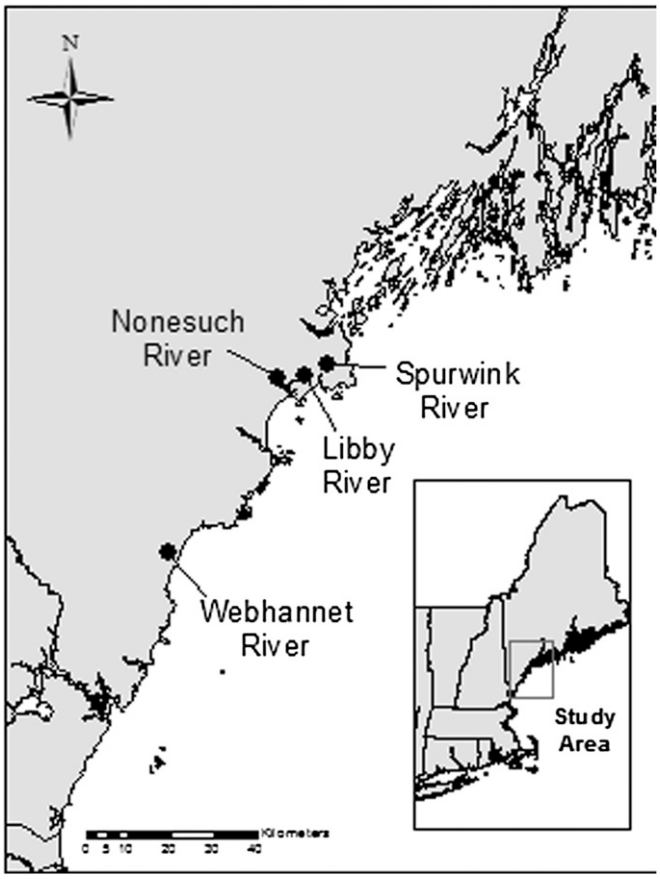

Fig. 1. Map of coastal Maine and location of field sites.

MATERIALS AND METHODS

***Site description*—**Four marshes in southern Maine were systematically surveyed for stand-scale clonal structure of *P. australis*. Marsh sites were in the Nonesuch (W 70.326°, N 43.580°), Webhannet (W 70.585°, N 43.286°), Libby (W 70.310°, N 43.563°) and Spurwink (W 70.250°, N 43.589°) Rivers. Maximum and minimum distances from marsh to marsh were 41 923 m and 2352 m, respectively. All sites have stands of native and introduced *P. australis* in proximity to each other. In the case of the Libby marsh, the introduced and native stands abutted each other and overlapped in some areas (E. L. G. Hazelton, personal observations). The marshes are back barrier dune systems and are well suited for comparisons of lineages among stands within the respective marshes.

***Sample collection and DNA extraction*—**In the summer of 2008, samples were collected from stands in the Nonesuch River watersheds (Fig. 1). The remaining marshes were sampled in the summer of 2011. Leaves were collected from the nearest stem to each sample grid point.

Along the Nonesuch River, we laid out a 1.5×6 m sampling grid, to capture detailed spatial structure, within two adjacent stands of *P. australis*. The use of spatially systematic sampling schemes is not new to clonal plant ecology (Douhovnikoff et al., 2005); however, this is the first use of the approach with *Phragmites*, and no previous spatial data were available on which to base our sample grid scale. As a result, a scale was selected that could cover the full extent of the stands in a systematic and spatially intense manner yet within the limited sample size available. At each grid point, the nearest stem was sampled by collecting fresh leaf material. A total of 58 samples were collected from the native stand, and 57 samples collected from the introduced stand. Results from the Nonesuch River indicated that sampling along a 5×5 m grid would be optimal in the remaining three marshes to capture as many genotypes as possible while still maintaining enough resolution for mapping by genotype.

Lineages were differentiated by morphological characteristics (Swearingen and Saltonstall, 2010), and microsatellite markers (Saltonstall, 2003). Prior molecular work identified the Nonesuch and Libby native stands as *P. australis* subsp. *americanus* (R. Meadows, Delaware Department of Natural Resources and Environmental Control, personal communication). Genomic DNA was extracted from leaves as done by Cullings (1992).

Microsatellite analysis—Ten microsatellite markers (single sequence repeats [SSRs]) developed for *P. australis* by Saltonstall (2003) were used to genotype all samples (PaGT4, PaGT8, PaGT9, PaGT11, PaGT12, PaGT13, PaGT14, PaGT16, PaGT21, PaGT22). The PCR included 5 ng DNA, 25 ng forward primer, 25 ng reverse primer, 200 μmol/L of each dNTP (Promega, Madison, Wisconsin, USA), 0.5 U *Taq* DNA polymerase (GibcoBRL, Grand Island, New York, USA), 20 mmol/L Tris-HCl pH 8.4, 50 mmol/L KCl and 1.5 mmol/L $MgCl_2$. Cycling conditions were 94°C for 2 min; 35 cycles of 94°C for 40 s, 54°C for 1 min, 72°C for 2 min; 72°C for 20 min. Amplified DNA was analyzed according to PE Applied Biosystems protocols on an ABI Prism 3100 DNA Sequencing System using Genemapper software (Applied Biosystems, Foster City, California, USA).

Using the programs PAUP* 4.0b10 (Swofford, 2003) and GENODIVE (Meirmans and Van Tienderen, 2004) software, genetic fingerprints were compared and clonal identity assigned per Douhovnikoff and Dodd (2003) based on matching of genotypes. In earlier work, a small number of markers were found to have adequate resolving power for disproving clonality and identifying genetically distinct samples (Kettenring and Mock, 2012). Genetically distinct samples may not be the immediate result of sexual reproduction, but distinct genotypes are originally derived from sexual recruitment.

As is common in clonal plant ecology, percentage distinguishable (PD) values were calculated as a metric of clonal diversity (Ellstrand and Roose, 1987). A PD value approaching zero indicates a hardly distinguishable set of samples and thus highly clonal; a value approaching 1.0 is highly distinguishable and not clonal. The PD values are a measure of diversity that averages the genotypes by sample size. As such, information about the distribution of clone sizes is lost. Thus, the usefulness of PD values for comparative purposes without an understanding of the skew in clone size distribution is questionable. For this reason, we also compared clone sizes as a proportion of sample size:

Relative clone size = no. of sample points in genet / no. sample points in stand.

In circumstances where clone size relative to the stand size may have important ecological implications, this metric is useful because it permits the analysis of the variance in genet size distributions while diminishing the effect of sample size. To analyze the direction and complexity of size distributions, we tested the null hypothesis that the structure of clonality in native and invasive stands was the same by calculating the differential Shannon entropy (DSE) as described by Godden and Bajorath (2001). It is important to note that these measures of clone size are based on the space occupied and not ramet density or biomass.

Any samples that do not match the genotypes of other samples in a stand are defined as singletons. If a singleton was found to differ by only one allele, it was retested starting at the extraction of DNA.

Singletons represent an interesting dilemma for the clonal plant ecologist by having a disproportionate effect on measures of diversity such as PD values relative to their size and ecological impact. For example, a stand with one singleton and 99 clonal ramets would have the same PD value as a stand with two 50-ramet clones. One could argue that in some situations, singletons should be discounted in the same way that genotypes shorter than breast height are often excluded in forest population studies. In some cases, singletons were excluded from calculations of genotype characteristics to test their influence.

A corrected Nei's diversity index (Simpson's index) was calculated for each site and lineage as a measure of clonal diversity and also used when randomizing alleles over individuals and testing the probability of finding the observed clonal identity results under random mating (GENODIVE: Meirmans and Van Tienderen, 2004). Within each marsh, pairwise comparisons of lineages were tested for statistically significant differences.

To compare genetic structure and spatial distribution, we calculated pairwise distance matrixes of genotype differentiation calculated using the Nei metric, and Euclidean distances were compared for spatial correlation using Mantel tests in the program Geno Dive at both the stand and marsh scale.

For all genotypes, a frequency based assignment test (Paetkau, 2004) was used to assess lineage assignments.

All marshes were ranked for level of clonality based upon genotype characteristics measured, and the rankings were tested using the Kruskal–Wallis rank order test (Kruskal and Wallis, 1952).

RESULTS

Using 10 microsatellite markers across the 714 samples (408 natives and 306 invasives), a total of 52 unique alleles were identified, 32 for the native lineage and 43 alleles for the invasive lineage (Table 1). Using the corrected Nei's diversity index, in a test randomizing the alleles over individuals in 1000 permutations, a low probability of finding the observed clonal diversity under random mating was demonstrated ($P_{GEN} < 0.001$). Overall, 125 genotypes were identified, 55 native and 70 invasive. Combined percentage distinguishable (overall PD = total genotypes/total samples) values were 0.18 (natives = 0.13, introduced = 0.23). Without singletons, the overall PD value was 0.08 (natives = 0.04, introduced = 0.13). No genotypes occurred in multiple marshes.

In all the marshes, both the introduced and native stands were made up of multiple genotypes and thus not monoclonal except for the Spurwink native stand, which consisted of one genotype. In a pairwise test of lineages within marshes, the allele numbers, number of multiramet genotypes, PD values minus singletons, Simpson's index, and Shannon diversity index were all significantly greater for the introduced lineage than those in native stands ($P < 0.05$, Table 1). Maximum total clone size and maximum clone size adjusted for area sampled were both significantly greater in the native stands.

Relative clone sizes were significantly larger in native stands than in introduced stands as tested by nested ANOVA ($F_{1, 42} = 12.69$, $P < 0.05$). The test of differential Shannon entropy rejected the null hypothesis that the clonal size distribution observed was due to random chance ($H = 0.27$, df = 54, $P > 0.0001$), and the distribution in the native was skewed toward larger clones. Variation in proportion of singletons was broader in native stands (0.22 SD) than introduced stands (0.06 SD).

While there were consistent lineage differences within each marsh, there also was important and consistent variation across marshes in genotype characteristics. In a rank order Kruskal–Wallis test of genotype characteristics associated with diversity, across marshes with lineage data pooled, significant differences ($H = 48.86$, df = 3, $P < 0.001$) were found. Libby scored highest (1.5 mean, 0.512 SD) followed by Nonesuch (1.6 mean, 0.512 SD), while Webhannet (3.1 mean, 0.478 SD) and Spurwink (3.66 mean, 0.478 SD) were consistently ranked lower. In each marsh, the largest clone detected was native.

Genotypes were spatially clustered based on correlated Mantel tests of clonality and Euclidean distances. We excluded

TABLE 1. Clonal diversity measures for native and invasive stands at four sites in Maine.

	Native				Invasive					Mean	
Clonal diversity measures	Libby	Webhannet	Spurwink	NoneSuch	Libby	Webhannet	Spurwink	NoneSuch	*F*	Native	Invasive
N samples	89	170	91	58	109	115	25	57		102	77
Alleles no.	29	13	12	27	37	31	29	36	**5.29**	**20**	**33**
N genotypes	21	2	1	31	35	11	5	19	13.25	14	18
N genotypes (less Singletons)	8	2	1	4	18	8	3	10	**3.84**	**4**	**10**
Largest clone (sample points)	27	158	91	25	13	69	20	9	**45.00**	**75**	**28**
Largest clone (% of *N* samples)	30	93	100	43	12	60	80	16	**0.08**	**67**	**42**
Singletons	13	0	0	27	18	3	2	6	14.39	10	7
Singletons (% of *N* samples)	15	0	0	47	17	3	8	11	0.24	15	9
PD value	0.24	0.01	0.01	0.53	0.32	0.10	0.20	0.33	0.30	0.13	0.23
PD value (less singletons)	0.11	0.01	0.01	0.13	0.20	0.07	0.13	0.20	**0.03**	**0.04**	**0.14**
Genotype diversity (Simpson's index)	0.82	0.13	0.00	0.80	0.94	0.59	0.42	0.92	**0.22**	**0.44**	**0.72**
Shannon's index	1.07	0.11	0.00	1.18	1.46	0.62	0.48	1.19	**0.27**	**0.59**	**0.94**

Notes: Boldfaced values differed significantly in a pairwise comparison between native and invasive stands within each marsh ($P < 0.05$). Mean percent distinguishable (PD) values were calculated by dividing the total number of genotypes by the total number of samples.

Spurwink native from this analysis due to its stand uniformity. The Mantel tests of Nei genetic distances and Euclidean distance showed a mean correlation of 0.14 for native species and 0.20 for invasive species; however, the variation was much greater for the native (0.189 SD) than the introduced (0.083 SD). The greatest correlations (r = 0.31–0.36) were found for both Libby stands, and the average was r = 0.18 across all stands. No significant difference in spatial structure was found between lineages.

DISCUSSION

Clonal growth was less prevalent in the introduced lineage and is therefore not likely the primary explanation for its invasive distinction in the region studied. In every marsh system, the introduced stands were more clonally diverse. These results are consistent with the clonal diversity observations of Kettenring and Mock (2012) on conspecifics in western North America. Our regional findings indicate that the native lineage has the greater propensity for clonal growth, which may explain its resistance to invasive displacement.

Clonal size—Clonality is often identified as an advantageous trait in invasive plants (Lin et al., 2009; Kui et al., 2013). However, specialists and stress tolerators can also benefit from clonal traits that contribute to genet persistence, space consolidation, resilience to change, and resistance to competition.

The potential location of new ramet growth in response to local, past and present site conditions in a nonrandom fashion allows for optimization of clonal architecture (Cheplick, 1997; Gómez and Stuefer, 2006; Gómez et al., 2007; Louapre et al., 2012; Bittebiere et al., 2012; Benot et al., 2013). Ramet integration can be adaptive (Alpert, 1999) with resource sharing across the genet (Alpert, 1990), making possible the specialization of specific ramets to the resource they are best positioned to exploit.

Clonal integration is generally considered advantageous in heterogeneous environments (Wijesinghe and Handel, 1994). In addition to heterogeneity in resource distribution, marsh environments can also be heterogeneous in ecological interactions. For example, intraspecific or intragenotype competition is likely greater on the clone edge where ramets are more likely to come into contact with competitors. With increasing clone size, the area to perimeter ratio increases, resulting in a progressively smaller marginal cost per ramet for site consolidation.

Ramet redundancy provides a level of risk sharing so that any stochastic disturbance or stress will have a lower likelihood of eliminating the entire genotype. For plants that follow a germination-to-senescence life history, the most vulnerable stage is during generational transition when seedlings are exposed to a broad range of mortal threats. These transitions are opportunities for more competitive species. Clonal reproduction is an alternative to the costs of sexual reproduction, avoids the risks associated in generational turnover, and with an indefinite lifespan, gives a squatter an open-ended timeline for site occupation.

All of these benefits increase with increasing size and have the potential to build to a considerable level of inertia (Arnaud-Haond et al., 2010), which may explain why native stands have not been overrun (Kettenring and Mock, 2012, Taddeo and deBlois, 2012) despite the fact that the introduced lineage has been ranked higher in all tested measures that might indicate the stronger competitor (Mozdzer and Megonigal, 2012; Mozdzer et al., 2013). In some situations, the jack-and-master competitive advantage of the introduced *Phragmites* may be small enough that it can be resisted through inertia. Studies predict, however, that competition in tandem with anthropogenic sources of N, CO_2, or disturbance could shift that balance in favor of the introduced lineage (Mozdzer et al., 2013).

Clonal size distribution—The greater the skew in size classes, the greater the ecological and genetic relevance of the largest genotype. The native clonal size distribution was significantly skewed to the larger size classes, whereas the introduced genotypes were more evenly distributed among moderate clone sizes. This broader range was also indicated by the greater standard deviation values of clone sizes in the native lineage.

An Allee effects model (Fig. 2B) predicting a low initial stand diversity that increases over time is often proposed for *Phragmites* stand development (McCormick et al., 2010; Hazelton et al., 2014). Several factors such as high levels of within-stand diversity detected in both lineages and no indications of inbreeding despite low effective population size argue against this model being appropriate for the sites measured here. The Allee effects model would suggest the native stands are relatively recent colonization events despite their greater size and likely longer history in the region. There was also a lack of the appropriate germination sites necessary for continued new recruitment, and in cases where local germination may be possible, those smaller genotypes would come into competition with much larger preexisting clones.

An intraspecific version of the initial floristic model (Hobbs and Legg, 1984), which we refer to as an initial genotypes model (Fig. 2A), better fits our results. Stand development begins with colonization by sufficient seed to result in genotypic diversity. Over time, genetic diversity is reduced due to rare seedling establishment and increasing intergenet competition (Zeidler et al., 1994; Koppitz and Kuhl, 2000; E. L. G. Hazelton et al., unpublished manuscript). This pattern of development has been observed for other clonal plants (Ellstrand and Roose, 1987) in a range of systems including riparian zones (Douhovnikoff et al., 2005), grasslands (Lehmann, 1997), and forests (Romme et al., 2005). The implication is that older stands will have less genotypic diversity.

A single genotype can maintain itself, and even expand, but without neighbors within pollination range, pollination limitation continues to limit gene flow and genetic diversity on a population scale (McCormick et al., 2010). When considering the extent of clonal growth we observed in the native stands, the level of diversity detected here and in other studies is greater than would be expected (Saltonstall, 2011) and is likely a good example of remnant regional dynamics as described by Eriksson (1996). Due to the great longevity of genotypes, connectivity to regional dynamics is maintained via intermittent periods of co-occurring local populations, and as a result, gene flow periodically continues.

Singletons—Despite their limited ecological impact, singletons can be informative about stand dynamics. The presence of singletons in introduced stands is relatively consistent. Native stands, on the other hand, comprise a comparable if not larger percentage of singletons or none at all. The number of singletons may be a reflection of the local disturbance history of each site. Facultatively clonal plants including *Phragmites* are well documented to capitalize on physical disturbance for sexual recruitment. Increases in *Phragmites* area are often associated with physical disturbance such as wrack (Minchinton, 2002) or

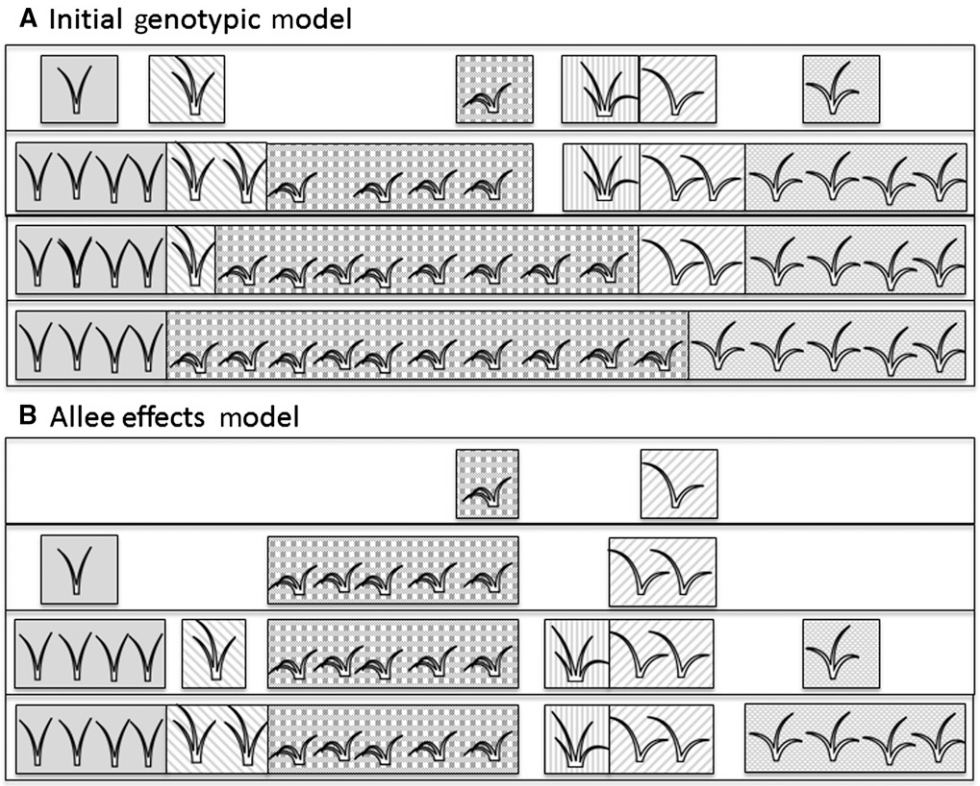

Fig. 2. Two models of *Phragmites* stand development. Time progresses from the top rectangle (initial state) toward the bottom rectangle (final state) in each model. (A) Initial genotypes model. Most genets are present at colonization, and as clones grow, competition reduces diversity. (B) Allee effects model. A small number of genets with low diversity expand through clonal growth until new recruits add enough diversity to promote outcrossing.

a water level drawdown (Alvarez et al., 2005; Tulbure and Johnston, 2010). If the presence of introduced *Phragmites* is an indicator of recent disturbance, it is also likely that the same disturbance could promote seed germination in the native. In fact, we only detected singletons in native stands Libby and Nonesuch that are directly adjacent to invasive stands, suggesting that disturbance is important for germination in both lineages.

It is possible that lack of singletons is another indicator of the initial genotypic model, reflecting native stand age or time since last disturbance. Singletons have either died off over time or succeeded in clonal growth (Fig. 2). Singleton genotypes are the most susceptible size class to competition, resource limitation, stochastic risk, and other factors that might lead to mortality. *Phragmites* clonal richness decreases with stand age (Čurn et al., 2007; Křiváčková-Suchá et al., 2007; E. L. G. Hazelton et al., unpublished manuscript), and the lack of singletons may indicate that the native stands have persisted in these locations for a longer time than the introduced stands within the same marsh. The ability of clonal plants to persist long after the senescence and decay of the original plant stem makes aging genotypes extremely problematic and is further complicated in nonwoody plants such as *Phragmites* with ramet components that die back annually.

Alternative explanations are that site quality in these situations is lower and barely conducive to seedling germination even after disturbance, these germination sites are at the edge of seed distribution range, or the lineages differ in seed germinability. A small number of genotypes might succeed in colonization and expand via clonal growth, which is less sensitive to resource conditions.

Marsh variation—While lineage was a consistent predictor of the within-site clonal diversity relative ranking, the marsh was a much stronger predictor of the absolute range of these values. These results suggest that lineage determines relative clonality but local conditions such as abiotic factors may be more important than lineage in determining absolute clonal character, consistent with observation in *Zostera marina* (Hughes and Stachowicz, 2009). Both natives and introduced respond to site variation in the same direction and maintain relative rank order. Measures such as PD values, mean clone size, and diversity measures can be considered with regards to their relationship to the extent of clonality. For example, as clonality increases PD values and diversity are likely to drop and mean clone size is likely to increase. Other studies have documented that anthropogenic impacts to the marsh abiotic environment can benefit the establishment and spread of introduced *Phragmites* (Bertness et al., 2002; Burdick and Konisky, 2003; Chambers et al., 2008; McCormick et al., 2010; Kettenring et al., 2011; and see detailed discussion by Hazelton et al., 2014), and it is very likely that a similar gradient of disturbance and nutrients are driving the clonal richness in our study marshes. In order, Libby, Nonesuch, Webhannet, and Spurwink reflect a consistent trend from measures related to low clonality through to high clonality in both lineages (Fig. 3). Evidently, the edaphic conditions that benefit the recruitment and clonal spread of introduced *Phragmites* also benefit native

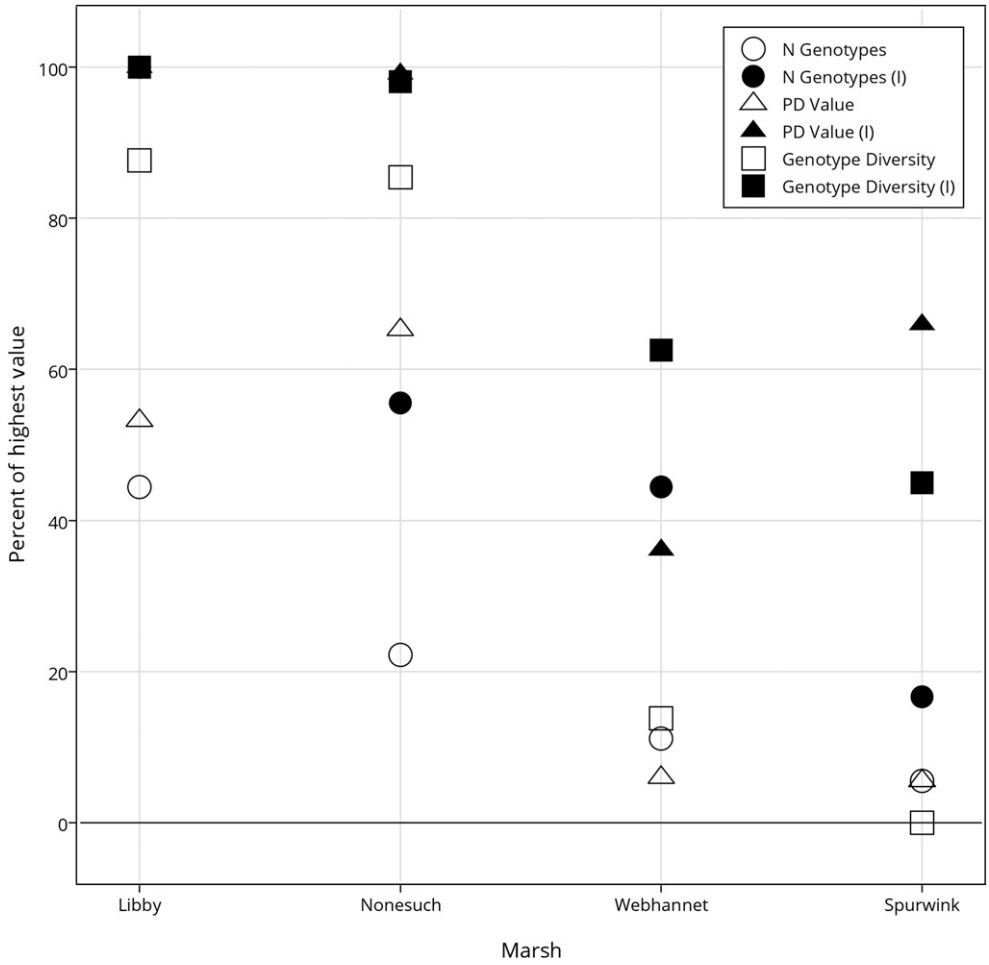

Fig. 3. Clonal diversity measures for natives (open symbols) and introduced (shaded symbols) for each marsh as a percentage of highest value measured.

Phragmites; however, direct measures of nutrients and disturbance are beyond the scope of the present study. Comparisons of the ecophysiology of the two lineages validate these findings in that the two lineages have similar nitrogen metabolism (Hazelton et al., 2010) and other growth-related parameters, only with a lag time for the native lineage (reviewed by Mozdzer et al., 2013).

***Conclusions*—**Introduced plants of *Phragmites* are highly clonal, and this clonality likely plays a role in its invasiveness. However, clonal size was greater in the native stands. Clonal growth appears to play an important role in space consolidation by native *Phragmites* and could explain why the introduced lineage, with its stronger competitive traits, has not replaced the native. Our results with regard to clone size, size distributions, singleton occurrence, and clonal architecture provide some evidence in support of an initial genotypic model. Over the expansive time scale available to clonal plants, local self-thinning of the initial colonizing genotypes will eventually result in a small number of very large clones. Observed levels of diversity could result from remnant regional dynamics maintained via intermittent periods of co-occurring local populations (Eriksson, 1996). While lineage is a factor in the extent of relative clonal growth, local marsh conditions appear to play an overriding role. More extensive sampling across a broader geographic range will help determine how representative these results are for differences in lineage clonal character.

The fitness costs of reproduction by clonal growth can include a limited ability to adapt to environmental and temporal heterogeneity (Alpert and Simms, 2002; Silvertown, 2008). The genotype is fixed, and as a result recombination of genetic material and associated natural selection are not available for the innovation and trial of new genotypes. How is it then that some facultatively clonal species are not only able to survive, but colonize, thrive, and expand in heterogeneous environments as we see in the introduced *Phragmites* lineage? We hypothesize that, in the case of *Phragmites* clonal genotypes, the answer lies in the great potential for phenotypic plasticity in the introduced lineage (Richards et al., 2006), possibly promoted by polyploidy. A broad capacity to acclimate to local conditions could balance the fitness costs of clonality.

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