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Rapid growth of a Eurasian haplotype of *Phragmites australis* in a restored brackish marsh in Louisiana, USA

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Abstract While numerous studies have documented patterns of invasion by non-indigenous plant species, few have considered the invasive properties of non-native genotypes of native species. Characteristics associated with specific genotypes, such as tolerance to disturbance, may mistakenly be applied to an entire species in the absence of genetic information, which consequently may affect management decisions. We report here on the incidence and growth of an introduced lineage of *Phragmites australis* in the Gulf of Mexico coastal zone of Louisiana. *P. australis* was collected from nine separate locations for inclusion in a series of growth experiments. Chloroplast DNA analysis indicated that specimens collected from four locations in the Mississippi River Delta represented the introduced Eurasian haplotype; the remainder represented the gulf coast haplotype. Three distinct genotypes, or clones, were identified within each haplotype via analysis using amplified fragment length polymorphisms, which also revealed reduced genetic diversity of the gulf coast clones compared to the Eurasian clones. Clones of each haplotype were planted along with three other native macrophytes at similar densities in a restored brackish marsh and monitored for growth. After 14 months, the Eurasian haplotype had spread vegetatively to cover about 82% of the experimental plots, more than four times the coverage (18%) of the gulf coast haplotype. Thus, the use of *P. australis* plantings for wetland restoration should consider the genetic lineage of plants used since our results indicate the potential of the Eurasian haplotype to grow rapidly at newly restored sites. This rapid growth may limit the establishment of more slowly growing native species.

Keywords AFLP · Clonal growth · Competitive ability · Genetic analysis · Genotypic variation · Invasive haplotype · *Phragmites australis* · Polymerase chain reaction · Restored wetland

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Introduction

Many studies have described patterns of invasion by non-indigenous, or introduced, plant species (e.g., Rouget and Richardson 2003; Thuiller et al. 2006) and have documented the impacts of such invasions on native species diversity and community functions (reviewed in Levine et al. 2003). Far fewer studies have considered the invasive properties of introduced genotypes of native species (Ellstrand and Schierenbeck 2000; Saltonstall 2002; Zedler and Kercher 2004). While invasions by introduced genotypes may

be rare in comparison to species-level invasions, they may also be underappreciated due to the difficulty of discerning the presence of such genotypes based solely on morphological characteristics. Genetic aspects should be considered for a more complete understanding of the factors involved in the invasive spread of native plant species. Invasion of North American wetlands by the perennial macrophyte *Phragmites australis* (Cav.) Trin. ex Stued. is a case in point. Molecular tools have detected an introduced lineage of *P. australis* (Saltonstall 2002; Saltonstall 2003a, b) in North America, and it has been speculated that genotypes of this lineage harbor more invasive properties relative to other genotypes (Lynch and Saltonstall 2002; Konisky and Burdick 2004; Vasquez et al. 2005). To date, however, there have been no controlled experiments that demonstrate the comparative invasive ability of the introduced lineage.

Phragmites australis, a genetically diverse species (Koppitz 1999; Kuhl et al. 1999), is one of the most widespread plant species in the world (Clevering and Lissner 1999). Native to North America (Orson et al. 1987; Kiviat and Hamilton 2001), *P. australis* is generally considered undesirable and invasive in many regions, where within the past century it has changed from a relatively minor component in diverse plant associations to an often dominant species that can form extensive monocultures (Chambers et al. 1999; Orson 1999; Rice et al. 2000). Numerous studies have documented the impacts associated with *P. australis* expansion in North American wetlands, including changes in plant community structure (Moore et al. 1999; Windham and Lathrop 1999; Burdick and Konisky 2003), the value of foraging and nesting habitats for birds (Benoit and Askins 1999; Trocki and Paton 2006), and in resident fish and macroinvertebrate populations (Weinstein and Balletto 1999; Angradi et al. 2001; Talley and Levin 2001; Osgood et al. 2003; Raichel et al. 2003; Buchsbaum et al. 2006; Hunter et al. 2006). While many studies have identified negative effects, others have indicated that *P. australis* invasions are likely to have negligible (Chambers et al. 1999; Talley and Levin 2001; Warren et al. 2001; Leonard et al. 2002; Windham and Ehrenfeld 2003) or even positive (Windham and Lathrop 1999; Rooth and Stevenson 2000; Findlay et al. 2003; Windham et al. 2003) impacts on fauna and ecosystem functions. Among the non-genetic factors implicated in the spread of *P. australis* in North America are the influence of natural (Minchinton 2002) and human-caused (Lynch and Saltonstall 2002; Minchinton and Bertness 2003) disturbances, hydrologic alterations and their related impacts on salinity regimes (Burdick et al. 2001; Bart and Hartman 2002, 2003; Chambers et al. 2003; Silliman and Bertness 2004; Buchsbaum et al. 2006), and competitive superiority compared to other marsh species (Burdick and Konisky 2003; Farnsworth and Meyerson 2003).

The potential role of introduced genotypes in the invasive spread of *P. australis* in North America has received increased attention since 2002 when, based on the sequencing of two non-coding chloroplast DNA (cpDNA) markers, Saltonstall (2002) determined that three distinct *P. australis* lineages are present in the North American flora. One lineage includes 11 closely related haplotypes unique to North America; these haplotypes are considered to be native (Saltonstall 2002, 2003a; Saltonstall et al. 2004). A second lineage, consisting of a single haplotype, is found along the Gulf of Mexico coast in North America and Mexico, as well as westward into California and south into northern South America (Saltonstall 2002). The geographic origin of this lineage is presently undetermined (Saltonstall 2002). A third lineage, also consisting of a single haplotype, is closely related to European and Asian strains of *P australis*; the geographical distribution of this haplotype has expanded over the past 100 years, and it is currently considered to be introduced in North America (Saltonstall 2002, 2003a).

Although recent studies have documented variation in morphological (Saltonstall et al. 2004; League et al. 2006) and physiological (Vasquez et al. 2005) characteristics among *P. australis* haplotypes, there are no published data on comparative growth rates of haplotypes in field settings. This information may help to explain the apparent competitive superiority of the Eurasian haplotype and its ability to supplant native species. In this paper, we report results comparing the growth of *P. australis* clones in a restored brackish marsh in coastal Louisiana, USA. This study was part of a larger wetland restoration field study that explored the benefits of planted versus naturally colonized vegetation communities; the field study also compared growth performance (measured as percent cover) of various plant species and clones

within species. Initiated prior to the documentation of the presence of the introduced *P. australis* lineage, the study entailed planting this species along with three other native macrophytes in a marsh that was restored by using substrate dredged from an adjacent waterway. While not an original objective of this study, the experiment was designed in a way that allowed documentation of the spatial distribution of *P. australis* clones over time. The questions we addressed in this paper are: (1) were different haplotypes of *P. australis* represented in the clones planted at the restored marsh?, (2) if more than one haplotype was represented, were differences in growth characteristics evident between or among haplotypes (under the null hypothesis of no difference)?, and (3) does genetic variation exist within haplotypes represented in the study?

Materials and methods

Plant collection

Specimens of four perennial emergent marsh species that are common and native to Louisiana were collected across the coastal zone of the state in 1998. In addition to *P. australis*, the species collected were *Distichlis spicata* (L.) Greene, *Schoenoplectus californicus* (C.A. Mey.) Palla, and *Schoenoplectus robustus* (Pursh) M. T. Strong. Data related to the latter three species are only marginally relevant to the data presented here and therefore receive limited attention in this paper. Plants were collected at widely spaced locations across ~340 km of the Louisiana coast in an attempt to sample existing ecotypic variation. The only criteria applied for selection were that the plants were apparently healthy and that the range of environmental conditions in which each species is typically found was covered. Several stems of *P. australis* plants with intact rhizomes were dug from the marsh sediment at nine locations; only stems connected by rhizomes were retained to ensure that a single genetic individual was represented. The plants were acclimated at a greenhouse facility in Lafayette, Louisiana (30°10′N, 92°00′W). Soil was washed from the roots, and plants were separated into individual ramets that included several culms and rhizome nodes supporting living roots. The ramets were planted in small pots (15 [diameter] × 12 cm) in a mixture of commercial potting soil and sand (6:1 ratio by volume). The pots were placed in large fiberglass tanks under common garden conditions (fresh water, flooding to 5 cm below the sediment surface) with high nutrient availability (commercial water-soluble fertilizer, 20–20–20 N : P : K added to tank water). The plants were vegetatively propagated for several generations; plants used in this study were maintained in common garden conditions for 3 years prior to initiating the experiment.

Study area

The study area was 65 ha of brackish marsh in the Barataria Basin of southeastern Louisiana (29°40′N, 90°06′W), which was restored in the summer of 2000 by using sediment dredged from the adjacent waterway, Bayou Dupont. The marsh had been in a degraded condition, with open water areas expanding in formerly vegetated habitat dominated by *Spartina patens* (Ait.) Muhl., *D. spicata*, and *Lythrum lineare* L. Three dredged-sediment locations along Bayou Dupont were selected in April 2001 (Fig. 1). Each location consisted of two planted sites, two not-planted sites, and a nearby reference (i.e., control) site that was not impacted by dredged sediment deposition. Only data collected at the planted sites are addressed in this paper. Six different specimens of each of the four species were planted, resulting in six replicates of the planted sites (hereafter called "units"). A series of parallel boardwalks (9 m × 25.4 cm) about 1.5 m apart and a 1-m high wire fence (9.5 × 7.75 m) were constructed to protect the units from trampling and from nutria (*Myocastor coypus*) herbivory, respectively.

The units were divided into a 7 × 4-cell grid system (Fig. 2). Each of the four species was randomly assigned to one of four columns, and within a column different specimens (i.e., from different collection locations) of a species were randomly assigned to rows 1 through 6. A duplicate of one of the six specimens for each species was planted in row 7 at one unit per site for destructive sampling of sediment accretion (data not reported). A 1-m^2 quadrat was defined near the center of each cell, and plantings consisted of two sets of 2–5 stems each placed into 15-cm diameter holes dug 30 cm apart and 15 cm from the quadrat center. The quadrat location (cell column and row) of each plant was recorded. Salinity

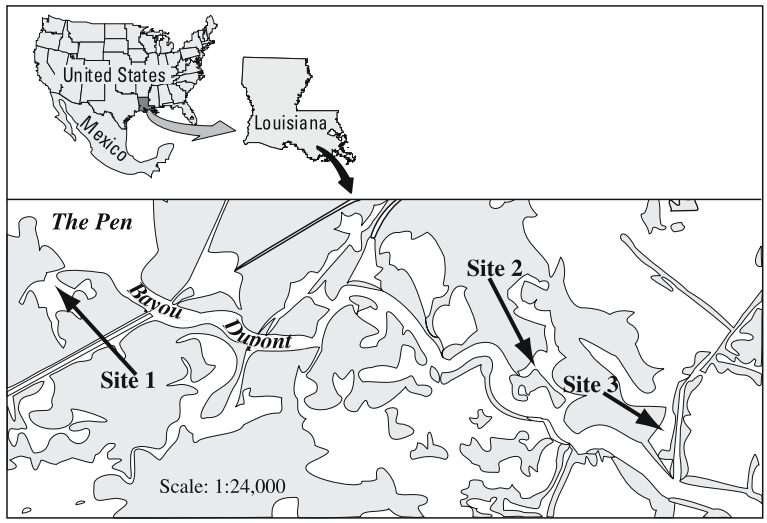

Fig. 1 Study site along Bayou Dupont, southeastern Louisiana, USA. The three sites where dredged sediment was deposited are indicated. Open water areas are indicated in *white*, including "The Pen," a constructed impoundment

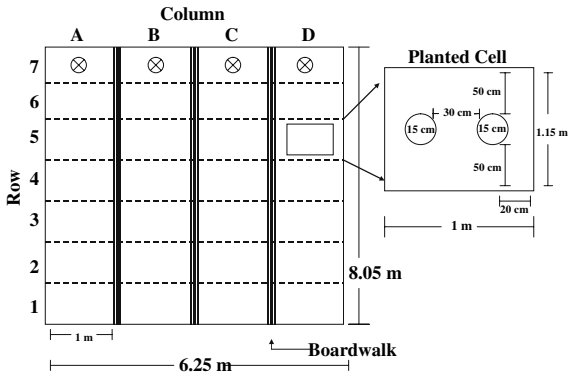

Fig. 2 Diagram of exclosure unit design, indicating the grid pattern of four columns (species) and seven rows (individuals). The *circles* in row seven indicate cells where destructive sampling for sediment accretion was conducted

at the site during the study ranged from 1 to 11 g/L, and water depth varied from 2 cm below to about 1 m above the marsh surface.

Data collection

Leaf tissue was collected from each original *P. australis* specimen (maintained in a greenhouse reference collection) in July 2002 and from each of the experimental grid cells at the study area where *P. australis* was growing; the time since planting was 14 months. A stem was selected from as near the center of each grid cell as possible. A total of 154 stems was sampled. Leaves were stored in plastic bags on ice in the field prior to returning to the laboratory where they were stored at −80°C until analysis. The identity of other plant species present in each cell was recorded.

Leaf tissue DNA was extracted by using a CTAB (hexadecyltrimethylammonium bromide)-based method (Saghai-Maroof et al. 1984; Rogers and Bendich 1985; Doyle and Doyle 1987). The origin of each sample (i.e., haplotype) was determined by using the polymerase chain reaction (PCR)-based method of Saltonstall (2003b). This involved the amplification of a non-coding region of the chloroplast genome, followed by a restriction digestion with the endonuclease *Hha*I. Only the Eurasian haplotype contains a suitable restriction site, whereas the gulf coast haplotype remains un-cut. Distinction among *P. australis* individuals was made by using a multi-locus genotyping method, amplified fragment length polymorphisms (AFLP), according to the methods of Travis et al. (2004). An initial screening of twelve primer combinations (*Eco*RI-ACG paired with *Mse*I-AAA, -AAC, -AAG, -AAT, -AGA, -AGC, -AGG, -AGT, -ATA, -ATC, -ATG, and -ATT) using 8–12 samples was used to identify the two primer combinations yielding the greatest numbers of polymorphisms (*Eco*RI-ACG/*Mse*I-AAC and *Eco*RI-ACG/*Mse*I-ATA).

Statistical analyses

Multivariate cluster analysis (NYSYS Version 2.1, Applied Biostatistics Inc., Port Jefferson, NY, USA)

(unweighted pair group method with arithmetic mean) of the multi-locus AFLP genotypes was used to visualize the relationships between the nine specimens. Relationships among the genotypes were assessed on a pairwise basis by using a simple coefficient of similarity (NTSYS Version 2.1) calculated as the proportion of shared AFLP markers (Lynch 1990). After matching each leaf sampled in the field to a haplotype, the number of grid cells occupied by each haplotype was summed within each replicate. The ratio change in occurrence for each haplotype, defined as the number of new cells occupied (final number occupied minus initial number of planted cells) divided by the number initially planted, was calculated. A *t*-test (SAS Institute Inc., Version 8, Cary, NC, USA) was used to compare the ratio change of occupied cells between haplotypes under the null hypothesis of equality. Chi-square tests were used to determine if growth varied by clones within a lineage based on initial planting ratio and the final ratio of occurrence in grid cells.

Results

Based on cpDNA analysis, the original collection of nine plants was composed of four representatives of the Eurasian (denoted as "M" by Saltonstall 2002) haplotype and five of the gulf coast ("I") haplotype. The M haplotype was found in the eastern section of the state, including the Mississippi River area, while the I haplotype was found across the coastal zone (Fig. 3). Genotyping of the original collection using AFLP techniques yielded 149 molecular markers, of which 41 (28%) were monomorphic across both the Eurasian and gulf coast lineages. Relationships among the nine genotyped collections are depicted in Fig. 4. The Eurasian and gulf coast haplotypes, or lineages, were distinguished by 96 markers that were absent from one lineage and either fixed or segregating in the other. Of the 89 markers available for genotyping the four M haplotypes, 20 (22%) were polymorphic, revealing three distinct genotypes, or clones (two of the original collections were identical). Pairwise comparisons of these clones showed them to differ by 10–16 markers. Of the 113 markers available for genotyping the five I haplotypes, just six (5%) were polymorphic, revealing that the three collections taken from the westernmost portion of Louisiana comprised just one genotype, or possibly two very closely related genotypes (one genotype differed by a single marker, which could have been the result of a recent mutation event); two distinct genotypes characterized the more easterly I haplotypes. Pairwise comparisons of the I clones showed them to vary by 3–5 markers.

Of the six *P. australis* specimens planted, three were the gulf coast (I) haplotype (3, 4, and 6), representing two distinct clones (Clone 3, Clone 4/6), and three were the Eurasian (M) haplotype (1, 2, and 9), also representing two distinct clones (Clone 1, Clone 2/9). After 14 months of growth, *P. australis* was found growing in 155 of a possible 168 grid cells over all six experimental units at the Bayou Dupont dredge site. Genetic analyses indicated that 26 and 126 representatives of the I and M haplotypes, respectively, were present (one sample was lost and two samples could not be assigned to a grid cell because of labeling errors; both of the mislabeled samples were haplotype M). Mean species richness per cell, excluding cells in row 7, was 2.97 ± 0.11 (±1 standard error, $n = 144$). Species other than *P. australis* were typically subordinate, and had relatively low cover values. *P. australis* was the only species present in 5 cells; in these cases, the species displaced was *S. robustus*. After 14 months of growth, changes in the occurrence of the I versus M haplotypes (Table 1) and ratio of change (Table 2) were evident. The grid cells planted with *P. australis* were originally comprised of 53.5 ± 1.6% (mean ± 1 standard error, $n = 6$) and 46.5 ± 1.6% of the gulf coast and Eurasian lineages, respectively. Final grid cells that supported *P. australis* growth were comprised of 17.5 ± 4.9% of the gulf coast lineage and 82.5 ± 4.9% of the Eurasian lineage. A *t*-test comparing change ratios was significant ($P < 0.0001$); the ratio was greater for the Eurasian (5.99 ± 0.61) than for the gulf coast (0.32 ± 0.43) haplotype.

Because each lineage was represented in the experiment by two distinct clones, we were able to further determine whether growth varied between clones within lineages. For the Eurasian lineage, a Chi-square test showed that the two clones spread to an equivalent number of grid cells over 14 months, taking into account their starting ratio of 2:1 ($\chi^2 = 0.3812$, $df = 1$, $P = 0.54$). Data from the 6 units were pooled for this test after it was determined from a Chi-square contingency analysis that they were not

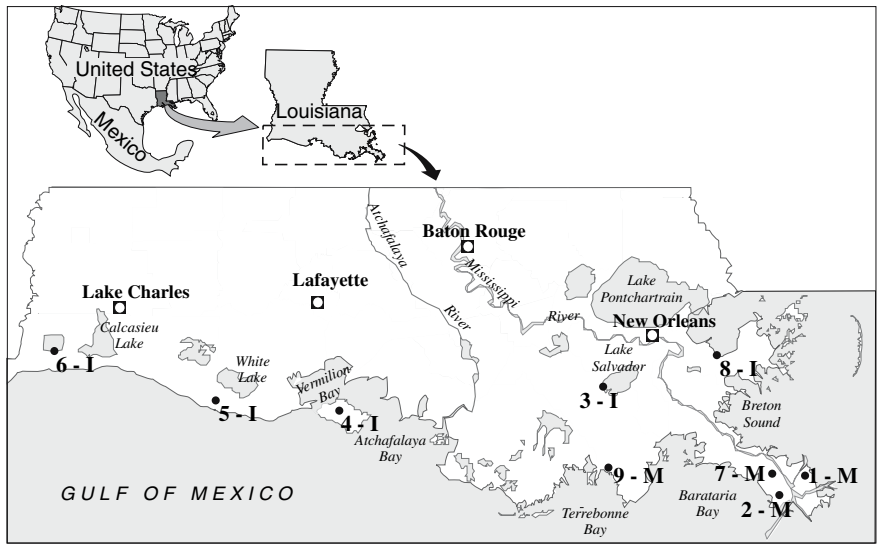

Fig. 3 Geographical distribution of haplotypes in a reference collection from coastal Louisiana, indicating plant number and haplotype identification. Eurasian haplotypes are denoted with an M, while gulf coast haplotypes are denoted with an I

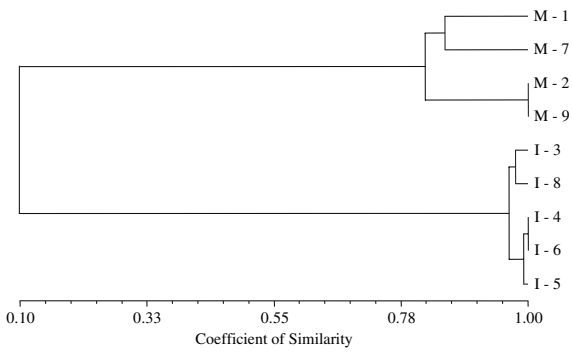

Fig. 4 A UPGMA (unweighted pair group method with arithmetic mean) cluster analysis depicting the relationships between nine *Phragmites australis* plant collections from the gulf coast of Louisiana based on 108 variable AFLP markers. Eurasian haplotypes are denoted with an M, while gulf coast haplotypes are denoted with an I

significantly different ($\chi^2 = 0.2730$, $df = 5$, $P = 0.99$). For the gulf coast lineage, of the 5 units within which some I haplotypes remained after 14 months, one of the two planted clones was identified in 24 of the 26 grid cells, and this was the clone that was planted at less than one-half of the frequency of the other. The more widely planted clone (clone 4/6) remained in only two of the nine grid cells occupied by the I haplotypes in unit 2A and was absent from the other units (a preponderance of zero values across most units made statistical comparisons problematic).

Table 1 Number of sample grid cells containing I (gulf coast) and M (Eurasian) clones of *P. australis* in May 2001 (at time of planting) and in July 2002

Site	Unit	May 2001		July 2002		July Number	
		I	M	I	M		Percent M
1	A	4	3	5	16	21	76
1	B	3	3	6	18	24	75
2	A	3	3	9	18	27	67
2	B	4	3	0	28	28	100
3	A	3	3	2	22	24	92
3	B	4	3	4	24	28	86

July number indicates the total number of cells that contained *P. australis*. Percent M indicates the percent of total cells containing the M haplotype in July 2002

Table 2 Ratio change in the number of grid cells occupied by I (gulf coast) and M (Eurasian) haplotypes of *P. australis* after 14 months of growth

Site	Unit	I Haplotype	M Haplotype
1	A	0.25	4.33
1	B	1.00	5.00
2	A	2.00	5.00
2	B	−1.00	8.33
3	A	−0.33	6.33
3	B	0.00	7.00

Discussion

Our study is the first to demonstrate experimentally that the introduced Eurasian haplotype is capable of a significantly greater rate of vegetative spread compared to the gulf coast haplotype. We recognize that the sampling methodology applied was conservative in the sense that the presence of a stem of one haplotype in the center of a grid cell did not exclude the possibility of the alternate haplotype occurring elsewhere in the cell. However, the systematic sampling method applied was unbiased and completely covered each unit. Therefore, the Eurasian haplotype appears to harbor superior intraspecific competitive ability as compared to the gulf coast haplotype, although the experiment was not explicitly designed as a competition study. Interestingly, the results of the field experiment are contradictory to results obtained from a greenhouse study using the same clones (Howard and Rafferty 2006). In that controlled study using individually potted plants, two of the M clones (clones 1 and 2) were less vigorous (lower stem height, lower aboveground and belowground biomass) than two of the I clones when exposed to constant salinity and flooding stressors over 3 months. Haplotype response was therefore quite different in the controlled conditions of the greenhouse compared to that in the fluctuating environmental conditions (e.g., salinity, water depth) at the restored brackish marsh. Because the greenhouse study was fertilized, variation in ability to acquire nutrients may be involved in the observed differences between haplotypes at the field site. Our study, conducted in an area of major hydrologic and soil disturbance, can be viewed as an example that supports hypotheses including disturbance as a factor leading to increased vulnerability to biotic invasions, in this case by increasing the availability of bare soil (Zedler and Kercher 2004). Clearly, further study is needed to clarify the specific mechanisms associated with competitive differences between the Eurasian and gulf coast haplotypes.

Other studies have compared growth and morphological characteristics of the M and native haplotypes in a greenhouse setting. In a study conducted with the M and two native haplotypes, Vasquez et al. (2005) demonstrated increased salt tolerance in the former. In contrast, Howard and Rafferty's (2006) greenhouse study showed that stem height of both M and I clones was decreased to the same extent by salinity of 10 g/L compared to 0 g/L. A greenhouse study including the M haplotype and a native haplotype conducted in concert with field observations indicated that the M haplotype had higher densities of emerging shoots early in the growing season, greater shoot height and biomass, and longer rhizome internode length; belowground biomass, however, was similar (League et al. 2006). Our results at the Bayou Dupont dredge site indicating vigorous growth of the M haplotype are consistent with this study.

While the presence of both the Eurasian (M) and gulf coast (I) haplotypes of *P. australis* in coastal Louisiana has previously been verified (Saltonstall 2002), we provide the first evidence of the occurrence of distinct clones of both lineages. Our results complement the work of Hauber et al. (1991), who recognized distinct *P. australis* morphological types, called "patch" and "background," in the Mississippi River Delta (MRD) based on signatures from infrared aerial photography. Allozyme analyses showed that these types correspond to two electrophoretic phenotypes; they also identified a third phenotype from outside the MRD. They speculated that the background MRD phenotype may be an invasive form related to strains invading marshes in the northeastern United States; a later study, however, was not able to verify this (Pellegrin and Hauber 1999). Using infrared aerial photographs and the assistance of a biologist (P. Deshotel, Louisiana Department of Wildlife and Fisheries) familiar with plant communities of the MRD, we collected specimens of both patch and background clones for our study. Our analyses using the more precise AFLP technique indicated that both were distinct clones representing the Eurasian haplotype.

Insight into the competitive ability of clones within haplotypes was also provided by our study. The two M clones were similar in that they spread to an equivalent number of grid cells over 14 months. Despite zero values prohibiting statistical analysis of I haplotype data, results were unequivocally in favor of the initially more uncommon gulf coast clone (clone 3) as the more robust clone, although both of the I clones used in the experiment performed poorly compared to the M clones. If the gulf coast lineage was originally founded by just one or a few clones (see below), it is possible that these clones are suffering from the effects of prolonged inbreeding,

perhaps exacerbated by a heavy mutational load built up through prolonged vegetative propagation (D'Amato 1997; Klekowski Jr 1997).

The Eurasian haplotype in our study was associated with major shipping channels, either surrounding the Mississippi River or along the edge of the Houma Navigation Canal (clone 9, Fig. 3). Thus, as has been speculated for the northeastern United States (Metzler and Rozas 1987; Saltonstall 2002), it is likely that the Eurasian haplotype was introduced to the MRD through ship packing materials or ballast, perhaps as early as the late nineteenth century. Literature from the early to middle part of the 1900s described *P. australis* in Louisiana as a species that occurred in mixed communities (Penfound and Hathaway 1938); small patches that occurred in the MRD were suggested to have originated from temporary blinds constructed by waterfowl hunters (O'Neil 1949). By 1970, expansive stands of *P. australis* were noted in the MRD (Chabreck and Palmisano 1973), suggesting that the M haplotype had become dominant by this time. There apparently have been multiple introductions, or a single introduction involving multiple clones, as the relatively large proportion of AFLP markers distinguishing genotypes within the M haplotype (up to 18%) would be unlikely to have arisen through repeated self-fertilization by a single introduced clone or by a process of somatic mutation occurring over a relatively short time span.

Our study is consistent with allozyme analyses indicating low clonal diversity within the gulf coast (I) haplotype. Using allozymes, Pellegrin and Hauber (1999) found that *P. australis* populations along the Gulf of Mexico coast from Texas to the Florida panhandle, excluding the active MRD, shared a single multi-locus phenotype. Although our AFLP analysis revealed at least three distinct I clones, they were extremely similar and shared just 3–4 of 113 total markers. Low clonal diversity of this haplotype suggests that the *P. australis* I lineage may be a geologically recent introduction to the Gulf of Mexico coast; this idea is supported by Saltonstall (2002), who noted that the I haplotype is not divergent from a lineage common in South America and also found in Asia and Australia. As indicated by our results, the founding gulf coast lineage of *P. australis* must have consisted of an extremely limited number of clones, or perhaps even a single clone that has diversified solely through a process of somatic mutation. The 5% of AFLP markers that were polymorphic within the I lineage could easily have resulted from a series of random mutations occurring over the span of several hundreds or thousands of years, since neutral marker loci such as AFLPs are not under selection and therefore have higher observed mutation rates than adaptive loci (Kimura 1983).

No evidence of genetic exchange between the gulf coast and Eurasian lineages of *P. australis* in Louisiana was indicated in our study. In fact, these lineages were so highly differentiated, with nearly 65% of $\sim$150 AFLP markers distinguishing them (Fig. 4), that it is not unreasonable to hypothesize that there may be reproductive isolating mechanisms between them. Our results therefore support the recent contention of Lambertini et al. (2006) that species status for the gulf coast and its related South American lineage should be considered. Previously, Saltonstall et al. (2004) recommended referring to the gulf coast lineage as *P. australis* var. *berlandieri* (E Fourn.) CF Reed. Evidence indicates, however, that limited sexual outcrossing between the dominant genotypes within the MRD has occurred (White et al. 2004). In addition to the dominant (patch and background) genotypes, White et al. (2004) identified two genotypes based on allozyme analyses that apparently resulted from a cross between the dominant genotypes. Our results suggest that it is probable that all four of the genotypes identified in that study belong to the Eurasian lineage.

Conclusions

Overall, our results indicate that there is a high potential for the Eurasian *P. australis* lineage to displace the gulf coast lineage in the northern Gulf of Mexico. This should be of particular relevance in the ongoing controversy over *P. australis* management in North America (reviewed in Rooth and Windham 2000; Ludwig et al. 2003; Weis and Weis 2003). Ludwig et al. (2003) suggested that effective management of *P. australis* requires a solid scientific foundation along with value judgments and assessment of the feasibility of possible actions. The increased primary productivity, decreased water depth, and high sediment accretion associated with large stands of *P. australis* may make the use of this

species an attractive option for restoring wetland habitats that are experiencing high rates of subsidence and/or accelerated sea-level rise in the Gulf of Mexico region. We suggest, however, that any proposed actions should consider the probability that the Eurasian lineage of *P. australis* has the potential to rapidly overgrow wetland restoration sites in the region, particularly if it is intentionally planted on uncolonized substrates. This finding, in concert with the findings of other researchers showing the resistance of *P. australis* monocultures to colonization by native species, suggests a strong possibility for the alteration of native gulf coast vegetation communities and their associated fauna.

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