

Clonal Differences in *Phragmites australis* from the Mississippi River Delta

DAVID A. WHITE^{1,*}, DONALD P. HAUBER¹, AND CRAIG S. HOOD¹

Abstract - In the active delta of the Mississippi River, *Phragmites australis* occurs in large contiguous stands of predominantly two clonal genotypes. We determined morphological variability among and within clones in this environment. Eight morphological variables were measured on culms from eight clonal populations within three subdeltas. Six populations were from the two dominant genotypes, whereas two populations were of two recombinant genotypes. All eight populations were genetically assessed from previous isozymic analysis. Culm, leaf and panicle morphology varied significantly between the two predominant genotypes, whereas the morphology of the two recombinant genotypes generally fell intermediate to that of both dominant genotypes. Morphological differences found within genotypes among the three subdeltas demonstrated phenotypic plasticity within *P. australis*. Morphological variability across subdeltas is likely the result of one or several environmental factors related to water depth or substrate quality.

Introduction

In Europe, because of its economic importance and dominance in wetlands, the clonal plant *Phragmites australis* (Cav.) Trin. ex Steud. (common reed), has been studied extensively (Haslam 1972, Ostendorp 1989, Van der Toorn 1972). Subsequently, work on the species has occurred in the United States (Hauber et al. 1991, Meyerson et al. 2000, Saltonstall 2002), primarily related to its invasiveness (Chambers et al. 1999). The genetic diversity, ecophysiology, growth dynamics, and general spread of the species have been the focus of recent research. *Phragmites* is a polymorphic species (Kühl et al. 1999) affected both by genetic factors and the environment (Clevering and Lissner 1999). Both water depth and salinity have been shown to impact its morphology (Coops et al. 1996, Hanganu et al. 1999, Yamasaki and Tange 1981). Clonal growth of the species sometimes produces stands of distinguishable morphological types. Clones of the reed have been variously named using informed descriptors in at least two different regions of the world, e.g., giant/fine from the Danube River delta (Hanganu et al. 1999) and background/patchy from the Mississippi River delta (Hauber et al. 1991).

We began research in the Mississippi River delta to explain landscape scale patterns in *Phragmites* seen on high and low altitude aerial

¹Department of Biological Sciences, Loyola University, New Orleans, LA 70118. *Corresponding author - dawhite@loyno.edu.

photographic imagery showing monoclonal stands of several genotypes (Fig. 1; Hauber et al. 1991). To date, over 106 populations of *Phragmites* from across the entire delta have been analyzed electrophoretically (Fournier et al. 1995). Most of the delta populations are identified as ‘background’ or ‘patchy’ because of their growth patterns. The patchy populations are usually found as circular patches imbedded within a surrounding landscape dominated by the background clonal type. However, a few populations are electrophoretically different from these two dominant genotypes. These different populations are small, often only about 1 ha in size, and, with few exceptions, determined to be monoclonal by sampling of culms along transects through the populations. Subsequent electrophoretic analysis indicates that they are most likely derived by hybridization between the common background and patchy genotypes. We refer to these as “recombinants,” and as many as seven different recombinant monoclonal genotypes have been identified throughout the delta (White and Hauber 1998). The discovery of these few recombinants was surprising because no seed production or seedlings have been seen in any of the delta populations over many years of field work.

From these general observations on the delta populations of *Phragmites*, several questions developed. Can we easily quantify the distinctive morphologies of the two most common isozymic types of



Figure 1. Low altitude photograph of a typical population of *Phragmites australis* in the Mississippi River delta. The dominant clonal genotypes growing in the delta are distinguishable; the more extensive “background” genotype surrounds the circular “patchy” clone. Dashed line illustrates a sampling transect for culms and panicles. For scale, the patchy clone is about 200 m across.

Phragmites (patchy and background) shown by their photographic signatures? Do recombinant types have distinctive morphology? Are the patchy and background types morphologically invariant in different regions of the Mississippi River delta? How do the genotypes fit within the range of known morphologies? What biological information on the ecology of *Phragmites* might be suggested by the answers to these questions?

Study Area

The delta of the Mississippi River (29°00'N, 89°15'E) is approximately 500 years old, consisting of four major passes that flow in different directions and give the 1400 km² region a “bird-foot” appearance. During the 1800s, the shallow bays between these passes experienced four levee breaches and consequently were filled by sediment, resulting in four large subdeltas (Fig. 2; Kolb and van Lopik 1958). Each subdelta is a complex of minor passes, man-made canals, vegetated land, mudflats, and ponds. The species associations of the vegetated marshland of these subdeltas are principally dependent upon the environmental gradients of elevation, substrate quality, and salinity

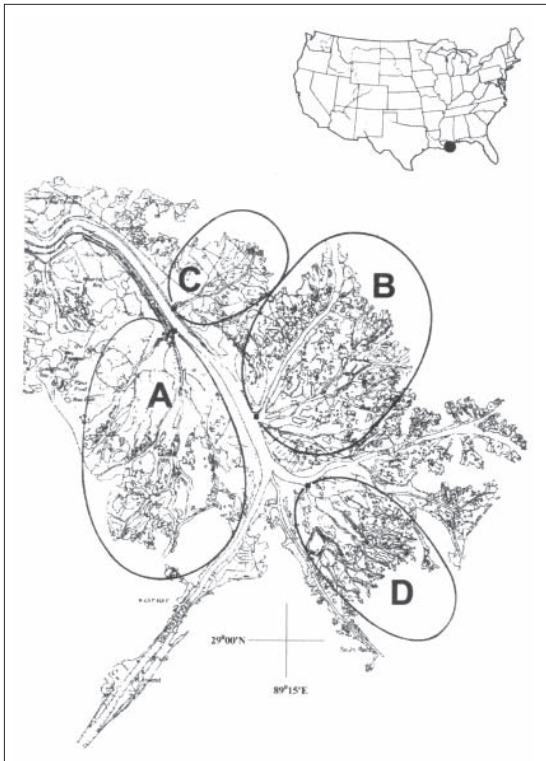


Figure 2. Map of the 500 year-old Mississippi River Delta depicting its 4 principle subdeltas; each began forming from a breach of the shoreline levee the year identified below. Modified from Coleman and Gagliano (1964). A = West Bay subdelta - 1838; B = Cubits Gap subdelta - 1862; C = Baptiste Collette subdelta - 1874; D = Garden Island Bay subdelta - 1891. For scale, the distance from the breach point of subdelta A to subdelta B is 11.5 km.

(White 1993, White and Hauber 1998). Because the spatial scale of these gradients can extend to over tens of km, each marsh plant association covers a large area. The marshes often are dominated by a single species from a list of few (White 1993), and virtually monospecific stands of *Phragmites* dominate the outer half of the delta lands.

Gulf of Mexico saltwater can be forced inland by storm events and mixed with the river's freshwater, thereby affecting the outer (downcurrent) reaches of each subdelta by "burning" or, in more severe cases, killing the aboveground portions of the plants. Since the early 1900s, in these peripheral regions of the delta, less salt-tolerant plants have been replaced by *Phragmites*, which has grown into the largest monospecific stands of the species in North America. The change in plant community is likely caused by the ability of *Phragmites* to both better withstand the effects of salt and harsh weather, and to vegetatively propagate and grow in a variety of water depths. Populations of common reed do occur in more interior regions of the delta as well. Our systematic isozymic sampling throughout the delta for genotypes and our careful scrutiny of photographic signatures have shown that the patchy and background clonal types are not only the most common, but also the most widely spread (Fournier et al. 1995, Hauber et al. 1991). The "patchy" genotype forms circular patches usually only several ha in size, and is interspersed within the more or less continuous and surrounding stands of the widespread "background" genotype (Fig. 1).

Over a number of years, the size of the "patches" has remained stable based on measurements from aerial photographs, supporting the contention that the background phenotype has grown around the patchy clones, rather than vice versa.

Methods

The field study was conducted in 1993–1994 in the three youngest of the four subdeltas: Baptiste Collette, Cubits Gap, and Garden Island Bay (Fig. 2), where the two dominant *Phragmites* clonal genotypes occur. The West Bay subdelta was excluded because our surveys over this subdelta found only the background genotype. With an eye to ease-of-access as an important consideration, we selected a subset of eight populations of *Phragmites* from our extensive survey across the delta. Each population was determined to be a single clone of one of four genotypes (patchy, background, recombinant 1, recombinant 2; Fournier et al. 1995). One population each of both the background and patchy genotypes was chosen from each of the three subdeltas. In the Cubits Gap and Garden Island Bay subdeltas, the two populations sampled abutted one another as illustrated in Figure 1. In the Baptiste Collette subdelta, no accessible clones of the two types could be found

near one another, so the nearest populations of the two genotypes (separated by 2 km) were sampled. In addition to these six populations of the principal genotypes, two of the recombinant populations were chosen from the Baptiste Collette subdelta. Each was isozymically distinct, consisting of a uniform genotype throughout (monoclonal). The four distinct genotypes identified from the Baptiste Collette subdelta were at sites of about the same elevation to control for the possible effect of depth of water. The eight populations identified for investigation were then revisited the following late October–early November to make plant collections at the time of peak biomass.

Culms ($n = 29\text{--}30$) were collected about 1 m apart along a transect into each population, avoiding “edge” effects particularly associated with open water (shoreline) areas, but also associated with interior clonal borders. Only culms with fully exerted panicles were selected to reduce the influence of age on analysis. Culms were clipped at the substrate level.

Owing to unsafe travel difficulties during the next year, panicles could only be collected from background, patchy, and the two recombinant populations in the Baptiste Collette subdelta. Because the background, patchy, and both recombinant clones individually reach peak anthesis over a short period in late autumn, the panicles were sampled on a single visit during each clone’s peak flowering period. We sampled the largest panicles in a clone, i.e., nearest to or at anthesis. Panicle sample sizes from the four populations varied from $n = 16\text{--}22$ because of availability.

In the laboratory, six vegetative measurements were taken on the field samples: stem width at base; stem length; stem oven-dried weight; width of third leaf from culm tip, length of third leaf, and oven-dried weight of third leaf. Panicles from the four Baptist Collette populations were measured for length and oven-dried weight.

Statistical analysis

Measurement data from culms and panicles from the eight clones (populations) were analyzed to address the questions about morphology. We focused on the four Baptiste Collette populations to assess differences among genotypes (i.e., background, patchy, recombinant 1, and recombinant 2), while we focused on the abutting populations of the background and patchy genotypes from Cubits Gap and Garden Island Bay subdeltas to look at phenotypic plasticity within genotypes. Univariate one-way ANOVAs were run on the Baptiste Collette data set to discern interclonal differences, and two-way ANOVAs were performed for the intraclonal study. The main effects for the two-way ANOVAs were genotype (i.e., patchy and background) and subdelta (Cubits Gap and Garden Island Bay). We eliminated culm width data

from the intracolonial statistical analyses because these data were missing from the Cubits Gap populations. The statistics package used for the ANOVAs was SPSS 10.1 for Windows (SPSS 2000).

In addition to the ANOVAs, patterns of morphometric variation among genotypes within a subdelta and within genotypes between subdeltas were investigated with Principal Components Analysis (PCA) performed using the software packages PC-ORD (version 3.20, McCune and Mefford 1995) and NT-SYSp (version 2.02, Rohlf 1997). In all analyses, stem and leaf measurements (culm length, culm weight, leaf width, leaf length, leaf weight) were standardized and a PCA was conducted on the cross-products correlation matrices (Greig-Smith 1983). Sample sizes were the same as described for the univariate analyses.

Three inter-genotype ordinations compared morphometric variation of all culms of the patchy and background genotypes collected in each subdelta (Baptiste Collette, Garden Island Bay, Cubits Gap). A fourth inter-genotype ordination compared the four genotypes (patchy, background, and two recombinants) from the Baptiste Collette subdelta. An intra-genotype ordination was used to investigate morphometric variation of all stems of the abutting clones of the patchy and background genotypes for Garden Island Bay and Cubits Gap subdeltas.

Results

Inter-genotype differences

Significant morphological differences were present among the four monoclonal populations (patchy, background, and two recombinants) of *Phragmites* in the marshes of the Baptiste Collette subdelta in the

Table 1. Mean population data from stems, 3rd leaves, and panicles of four clonal populations of four different genotypes of *Phragmites australis* collected 1993–1994 in the Baptiste Collette subdelta of the Mississippi River delta. The populations are scattered over a several km² area. Width and length measurements are in cm and weights are in grams. Figures with the same letter superscript within rows are not significantly different as determined by multiple comparisons tests at the 0.05 probability level.

	Patchy		Background		Recombinant 1		Recombinant 2	
	x	n	x	n	x	n	x	n
Stem								
Width	1.30 ± 0.038 ^a	29	1.31 ± 0.024 ^a	30	1.33 ± 0.031 ^a	29	1.39 ± 0.026 ^a	30
Length	459.1 ± 6.31 ^a	29	430.6 ± 3.20 ^b	30	443.5 ± 7.48 ^{ab}	29	492.7 ± 4.33 ^c	30
Weight	125.2 ± 5.95 ^{ac}	29	93.4 ± 3.95 ^b	30	105.9 ± 5.14 ^{ab}	29	109.8 ± 3.45 ^{abc}	30
3rd leaf								
Width	2.01 ± 0.062 ^a	29	1.96 ± 0.041 ^a	30	1.95 ± 0.058 ^a	29	2.08 ± 0.044 ^a	30
Length	51.9 ± 0.96 ^a	29	46.4 ± 0.58 ^b	30	46.0 ± 0.95 ^b	29	50.6 ± 0.51 ^a	30
Weight	0.69 ± 0.041 ^a	29	0.39 ± 0.021 ^b	30	0.59 ± 0.032 ^{ac}	29	0.51 ± 0.023 ^c	30
Panicles								
Length	35.1 ± 0.69 ^a	16	27.4 ± 0.50 ^b	20	25.7 ± 0.41 ^b	21	25.4 ± 0.61 ^b	22
Weight	7.20 ± 0.45 ^a	16	1.89 ± 0.13 ^b	20	1.56 ± 0.13 ^b	21	1.84 ± 0.21 ^b	22

Mississippi River delta. One-way ANOVAs showed a significant difference in six of the eight measured variables (stem length, $F = 23.8$, $P < .0001$; stem weight, $F = 7.7$, $P < .0001$; leaf length, $F = 14.6$, $P < .0001$; leaf weight, $F = 17.8$, $P < .0001$; panicle length, $F = 58.3$, $P < .0001$; panicle weight, $F = 115.7$, $P < .0001$). Stem width and leaf width did not differ significantly among the four populations (Table 1). The patchy stems averaged 28.5 cm longer (patchy = 459.1 cm; background = 430.6 cm), with stands of both types growing to about 4.5 m in height, and the dry weight of the patchy stems (125.3 g) was 34% more than the weight of the background stems (93.4 g). Stems from the two recombinant populations generally had intermediate mean lengths and weights.

Although morphometrics on panicles were collected independently and were not included in the PCA ordination, they helped to distinguish among the four populations from the Baptiste Collette subdelta (Table 1). During flowering it was easy to identify the patchy genotype because

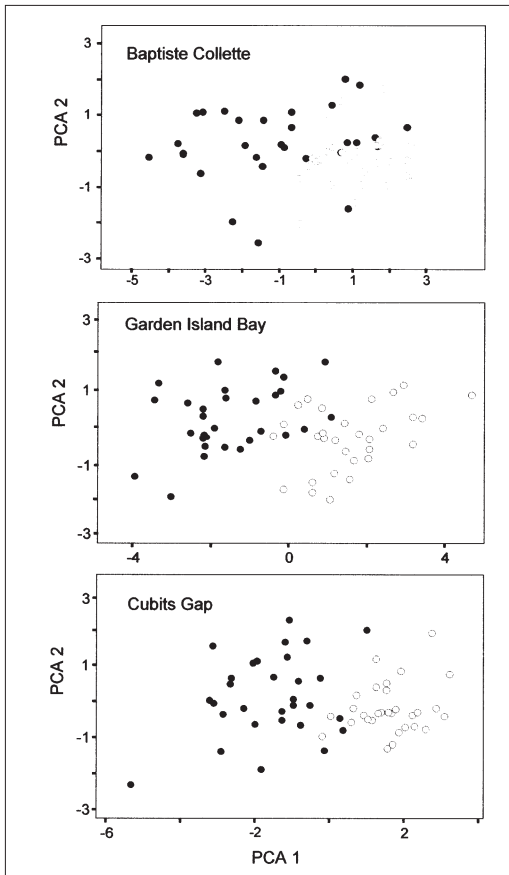


Figure 3. Plots of Principal Components Analysis (PCA) ordinations of five morphometric variables for patchy and background genotypes. Each plot depicts an ordination of 29–30 patchy and 30 background culms from each subdelta analyzed in separate PCAs. Symbols indicate monoclonal populations: solid circles = Patchy, open circles = Background. Baptiste Collette PCA results: PC 1 eigenvalue 3.290, 65.8% of variation; PC 2 eigenvalue 0.797, 15.9% of variation. Garden Island Bay PCA results: PC 1 eigenvalue 3.792, 75.8% of variation; PC 2 eigenvalue 0.754, 15.1% variation. Cubits Gap PCA results: PC 1 eigenvalue 3.685, 73.7% of variation; PC 2 eigenvalue 0.912, 18.2% variation.

the panicles were nearly four times heavier and nearly 10 cm longer than the other three genotypes. Flowering times of the populations differed in that the background type and the patchy type both flowered in a rather short period, the former 2–3 weeks earlier (late October) than the latter (early November), while the recombinant types flower for a longer period and overlap the times of the two dominant types.

The PCA ordinations of patchy and background genotypes within each of the three subdeltas showed these genotypes were morphometrically distinct (Fig. 3). In each of these three ordinations, the first two principal component axes accounted for a very large percentage of variation in their respective data sets (Baptiste Collette PCA, 81.7%; Garden Island Bay PCA, 90.9 %; Cubits Gap PCA, 91.9%). In all analyses, all five variables were negatively related to PC 1 (all eigenvectors > 0.4). Stem variables were positively related to PC 2 (> 0.4), whereas leaf variables were negatively related to PC 2 (> 0.4). The patchy genotype within each subdelta had taller and heavier stems with longer and heavier third leaves than did the background genotype.

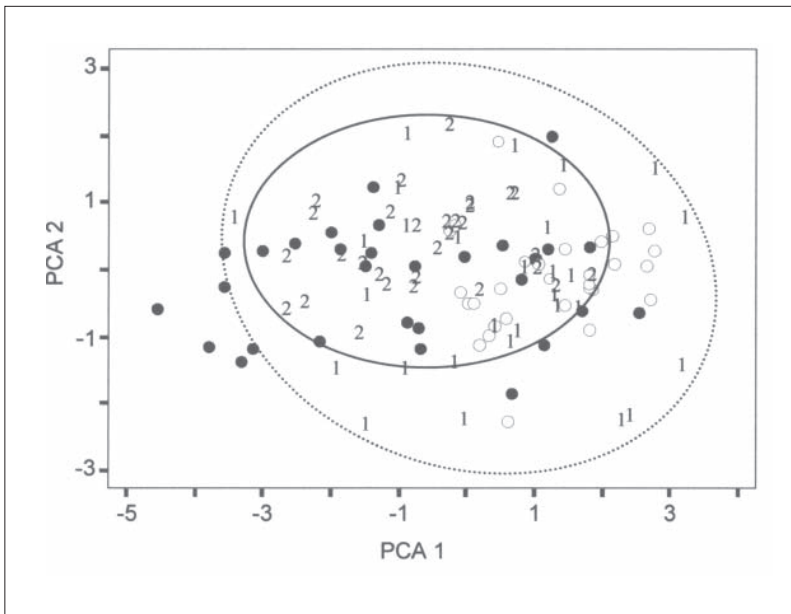


Figure 4. Principal Components Analysis (PCA) ordination of five morphometric variables for four genotypes (patchy, background, two recombinant populations, total $n = 118$ culms) within the Baptiste Collette subdelta. Symbols indicate monoclonal populations (solid circle = Patchy, open circle = Background, 1 = Recombinant 1, 2 = Recombinant 2) and the two ellipses encompass recombinant samples to aid visualization (dotted-lined ellipsis for R1, solid-lined ellipsis for R2). PC axis 1 eigenvalue 2.896, 57.9% of variation; PC 2 eigenvalue 0.894, 17.9% of variation.

The PCA ordination of the four genotypes (patchy, background, and two recombinant populations) from Baptiste Collette subdelta revealed that the recombinants overlapped the patchy and background genotypes significantly (Fig. 4). The first two principal component axes accounted for 75.8% of the overall variation. All five variables were negatively related to PC 1 (all eigenvectors > 0.4). Stem variables were positively related (> 0.4) and two leaf variables (leaf length and weight) were negatively related to PC 2 (> 0.4). The morphometric patterns evident in the PCA described above for patchy and background genotypes at Baptiste Collette (Fig. 3) were not affected by the inclusion of the two recombinant populations (Fig. 4). Moreover, the variability of the recombinant populations on the ordination broadly overlapped both patchy and background genotypes.

Intra-genotype differences

The morphology of patchy and background genotypes were compared between Cubits Gap and Garden Island Bay subdelta populations that abut one another (Table 2). The two-way ANOVAs showed a significant difference within genotypes among subdeltas (genotypes \times site) for one variable, stem length ($F = 22.37$, $P < .0001$). The remaining variables, stem weight ($F = 2.56$, $P = 0.113$), leaf width ($F = 1.98$, $P = 0.162$), leaf length ($F = 1.38$, $P = 0.242$), leaf weight ($F = 2.80$, $P = 0.097$) were not significantly different.

The PCA ordination of patchy and background genotypes at Garden Island Bay and Cubits Gap subdeltas illustrated some degree of phenotypic plasticity within each genotype (Fig. 5). The first two principal component axes accounted for 88.4% of the overall variation. All five variables were negatively related to PC 1 (all eigenvectors > 0.4), and they separate populations of each genotype across subdeltas (intra-genotype variation). This axis also separates the patchy and background

Table 2. Mean population data from stems and 3rd leaves of four clonal populations of two genotypes of *Phragmites australis* found in two sub-deltas within the Mississippi River delta. The two clonal populations from the same subdelta are growing abutting one another as shown in Figure 1. The "patchy" genotype occurs in discrete circular stands and usually is surrounded by the "background" genotype. $N = 30$ for each measurement.

	Patchy		Background	
	Garden Island Bay	Cubits Gap	Garden Island Bay	Cubits Gap
Stem				
Length (cm)	469.3 \pm 3.70	432.1 \pm 6.25	455.2 \pm 4.00	372.5 \pm 4.86
Weight (g)	116.7 \pm 3.85	109.5 \pm 3.40	77.6 \pm 2.88	61.9 \pm 1.67
3rd leaf				
Width (cm)	2.6 \pm 0.04	2.3 \pm 0.05	2.1 \pm 0.05	1.9 \pm 0.03
Length (cm)	59.4 \pm 0.66	54.7 \pm 0.83	47.1 \pm 0.92	44.3 \pm 0.68
Weight (g)	0.7 \pm 0.03	0.7 \pm 0.03	0.4 \pm 0.02	0.5 \pm 0.02

genotypes (inter-genotype variation). Stem variables were positively related (all eigenvectors > 0.4) and leaf variables were negatively related (leaf weight eigenvector > 0.5) to PC 2. This axis separates populations of each genotype across subdeltas and demonstrates intra-genotypic geographic variation. Populations of the background genotype exhibit a greater degree of morphometric separation from one another than do those of the patchy genotype.

Discussion

Morphological differences between the background and patchy genotypes of *Phragmites* in the Mississippi River delta are quantifiable and correspond to previously observed isozymic differences and infrared reflectance patterns (Hauber et al. 1991). The degree of genetic differentiation between background and patchy (Nei's identity = 0.836; Pellegrin and Hauber 1999) is considerable for conspecific populations of plants (Crawford 1990), and consistent with the statistically signifi-

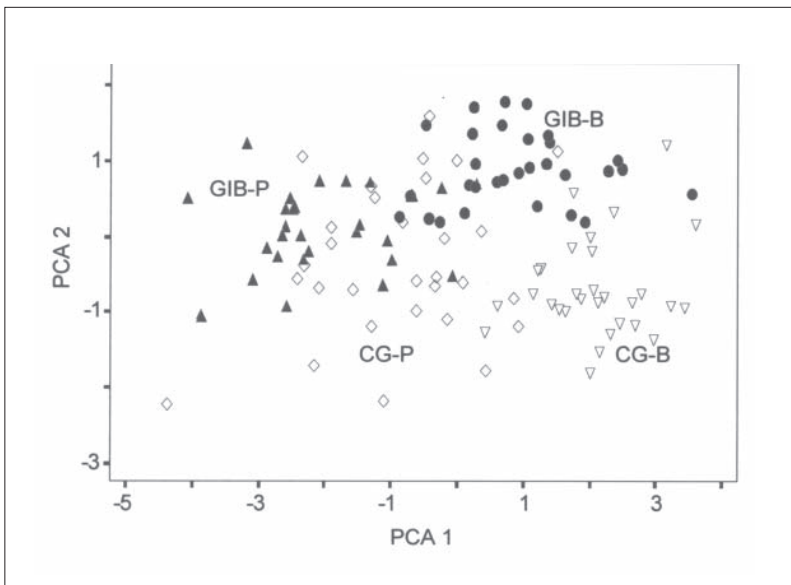


Figure 5. Principal Components Analysis (PCA) ordination of five morphometric variables for patchy (P) and background (B) genotypes within Garden Island Bay (GIB) and Cubits Gap (CG) subdeltas (total $n = 120$ culms). Symbols indicate mono-clonal populations and the subdelta location of samples: solid symbols used for Garden Island Bay and open symbols for Cubits Gap, i.e., solid triangle = GIB Patchy, solid circle = GIB Background, open diamond = CG Patchy, open triangle = CG Background. Placement of labels for sample populations (GIB-P, GIB-B, CG-P, CG-B) are provided to aid in visualization. PC axis 1 eigenvalue 3.583, 71.7% of variation; PC 2 eigenvalue 0.838, 16.8% of variation.

cant morphological differences in 6 of 8 characteristics analyzed in this study. Likewise, the two recombinant populations, which were originally identified by their isozymic profiles with alleles of both background and patchy genotypes, display centers of morphological variation overlapping the putative parents.

When comparing the morphological characteristics of the four genotypes studied from the Mississippi River delta to other studies of clonal *Phragmites* populations, several results are worth noting. The extreme size and weight of the patchy and recombinant 2 genotypes are large for most populations of *Phragmites*, but comparable to other reports of tallest forms from Europe (Dykyjová 1978, Paucă-Comănescu et al. 1999, Raicu et al. 1972). This is consistent with the recent genetic evidence indicating that background and patchy share the same chloroplast haplotype, which is European in origin (Saltonstall 2002). It is not known whether the presence of the background and patchy genotypes was the result of separate introductions. Regardless, the evidence points to their arrival sometime in the early to middle 1900s.

Morphological differences within genotypes are surprising considering all shoots of *Phragmites*, whether taken from the same population or from several kilometers away, are presumed genetically identical as a result of the isozymic analysis. There is a significant genotype x site interaction demonstrated in culm length and a clear separation of populations of each genotype across the different subdeltas, as exhibited by the PCA. Two possible explanations account for this discovery: 1) morphological differences reflect actual genetic differences not detected by electrophoretic methods (a universal problem with interpreting results), or 2) differences in morphology among the populations are a result of plasticity in the species either associated with a subdelta's history or simply locally developed, independent of the subdelta. Considerable plasticity in the species has long been known (Daniels 1991, Dykyjová 1978) and continues to be studied (Hanganu et al. 1999, Köhl et al. 1999, Rolletschek et al. 1999). To suggest that the isozymic genotypes from different sites are, in fact, genetically differentiated, but simply not detected electrophoretically, would imply isozyme differentiation is conservative. This scenario might seem possible if we were discussing a single isozyme genotype, such as in *Typha latifolia* (Mashburn et al. 1978). However, there are two widespread genotypes in the current study, so there would need to be an undetected genetic variation within each of these isozyme profiles, which does not seem likely.

Local environmental differences at the specific sites chosen in the three subdeltas likely explain the observed morphological differences. We observed differences in water depth at the sites suggesting that *Phragmites* from the Mississippi River delta maybe responding to depth of flooding, or a surrogate thereof (site elevation, substrate bulk density,

redox potential, nutrient availability). For years, European studies have attributed morphological differences between adjacent clones of *Phragmites* to growth in particular depths of water or to other hydrological conditions (Björk 1967, Dykyjová 1971, Dykyjová and Hradecká 1973, Vretare et al. 2001). More recently, because of the invasion of *Phragmites* along the northeast coast of the United States, studies are showing the species' tolerance to wide environmental conditions (Burdick and Konisky 2003, Chambers et al. 2003). To definitively test the impacts of different Mississippi River delta environments on morphology and invasiveness, we should take vegetative measurements on other populations of the background and patchy types growing under different hydrological conditions, particularly sampling several populations in the same subdelta.

This study is provocative in that the delta-wide dominance of *Phragmites* could reflect its ability to spread into diverse environments because of its observed plasticity. Future studies should also investigate growth strategies between the clones. The background clone might show a greater expansion rate into open habitat, whereas the patchy clones could be competitively superior once established, with the recombinant clones inferior.

Acknowledgments

This study was supported in part by grants to undergraduate student Thao Luu from the Mullahy Fund for Undergraduate Research in the Department of Biological Sciences, the NSF/Louisiana Board of Regents Summer Fellowship Program, and Sigma Xi. We thank Ms. Luu for the hard work in the field and conscientious lab work. Drs. M. Molvray and P. Kores were especially helpful in early data analysis and comments. The authors thank the U.S. Fish and Wildlife Service for use of boats and equipment for the collections. Both the U.S. Fish and Wildlife Service and the Louisiana Department of Wildlife and Fisheries granted generous access to the sites.

Literature Cited

- Björk, D. 1967. Ecological investigations of *Phragmites communis*: Studies in theoretical and applied limnology. *Folia Limnologica Scandinavica* 14:1–248.
- Burdick, D.M., and R.A. Konisky. 2003. Determinants of expansion for *Phragmites australis*, common reed, in natural and impacted coastal marshes. *Estuaries* 26:407–416.
- Chambers, R.M., L.A. Meyerson, and K. Saltonstall. 1999. Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquatic Botany* 64:261–273.
- Chambers, R.M., D.T. Osgood, D.J. Bart, and F. Montalto. 2003. *Phragmites australis* invasion and expansion in tidal wetlands: Interactions among salinity, sulfide, and hydrology. *Estuaries* 26:398–406.

- Clevering, O.A., and J. Lissner. 1999. Taxonomy, chromosome numbers, clonal diversity, and population dynamics of *Phragmites australis*. *Aquatic Botany* 64:185–208.
- Coleman, J.M., and S.M. Gagliano. 1964. Cyclic sedimentation in the Mississippi River deltaic plain. *Transactions of the Gulf Coast Association of Geological Societies* 14:67–80.
- Coops, H., F.W.B. Van den Brink, and G. Van der Velde. 1996. Growth and morphological responses of four helophyte species in an experimental water-depth gradient. *Aquatic Botany* 54:11–24.
- Crawford, D.J. 1990. Allelic data: Studies of populations and infraspecific taxa. Pp. 95–106. *In* D.J. Crawford (Ed.). *Plant Molecular Systematics*. John Wiley and Sons, New York, NY. 388 pp.
- Daniels, R.E. 1991. Variation in performance of *Phragmites australis* in experimental culture. *Aquatic Botany* 42:41–48.
- Dykyjová, D. 1971. Ecotypes and ecomorphoses of common reed, *Phragmites communis* Trin. *Preslia* 43:120–138.
- Dykyjová, D. 1978. Plant growth and estimates of production. Pp. 159–163. *In* D. Dykyjová, and J. Kvet (Eds.). *Pond Littoral Ecosystems: Structure and Functioning*. Springer-Verlag, New York, NY. 464 pp.
- Dykyjová, D., and D. Hradecká. 1973. Comparative investigation on the microclimate in two reed-bed biotypes and its relation to the ecotype, productivity and trophic conditions of habitat. *Polish Archives of Hydrobiology* 20:111–119.
- Fournier, W., D.P. Hauber, and D.A. White. 1995. Evidence of infrequent sexual propagation of *Phragmites australis* throughout the Mississippi River delta. *American Journal of Botany* 82(6-supplement):71.
- Greig-Smith, P. 1983. *Quantitative Plant Ecology*. 3rd Edition. Blackwell Scientific Publications, Oxford, U.K. 359 pp.
- Hanganu, J., G. Mihail, and H. Coops. 1999. Responses of ecotypes of *Phragmites australis* to increased seawater influence: A field study in the Danube Delta, Romania. *Aquatic Botany* 64:351–358.
- Haslam, S.M. 1972. Biological flora of the British Isles. *Phragmites communis* Trin. *Journal of Ecology* 60:585–610.
- Hauber, D.P., D.A. White, S.P. Powers, and F.R. DeFrancesch. 1991. Isozyme variation and correspondence with unusual infrared reflectance patterns in *Phragmites australis* (Poaceae). *Plant Systematics and Evolution* 178:1–8.
- Kolb, C.R., and J.R. Van Lopik. 1958. *Geology of the Mississippi Deltaic Plain-Southeastern Louisiana*. U.S. Army Engineers Waterways Experiment Station, Vicksburg, MS., Technical Report 2:3–483.
- Kühl, H., H. Koppitz, H. Rolletschek, and J.G. Kohl. 1999. Clone specific differences in a *Phragmites australis* stand. I. Morphology, genetics and site description. *Aquatic Botany* 64:235–246.
- Mashburn, S.J., R.R. Sharitz, and M.H. Smith. 1978. Genetic variation among *Typha* populations of the southeastern United States. *Evolution* 32:681–685.
- McCune, B., and M.J. Mefford. 1995. *PC-ORD. Multivariate Analysis of Ecological Data*. Version 3.20. MjM Software Design, Glenendon Beach, Oregon. 126 pp.
- Meyerson, L.A., K. Saltonstall, L. Windham, E. Kiviat, and S. Findlay. 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. *Wetlands Ecology and Management* 8:89–103.

- Ostendorp, W. 1989. "Die-back" of reeds in Europe: Critical review of literature. *Aquatic Botany* 35:5–26.
- Paucă-Comănescu, M., A.O. Clevering, J. Hanganu, and M. Gridin. 1999. Phenotypic differences among ploidy levels of *Phragmites australis* growing in Romania. *Aquatic Botany* 64:223–234.
- Pellegrin, D., and D.P. Hauber. 1999. Isozyme variation among populations of the predominantly clonal species, *Phragmites australis*. *Aquatic Botany* 63:241–259.
- Raicu, P., S. Staicu, V. Stoian, and T. Roman. 1972. The *Phragmites communis* Trin. chromosome complement in the Danube Delta. *Hydrobiologia* 39:83–89.
- Rohlf, F.J. 1997. NTSYS-pc. Numerical taxonomy and multivariate analysis system. Version 2.02. Exeter Software, Setauket, New York, NY. 28 pp.
- Rolletschek, H., A. Rolletschek, H. Köhl, and J.G. Kohl. 1999. Clone specific differences in a *Phragmites australis* stand II. Seasonal development of morphological and physiological characteristics at the natural site and after transplantation. *Aquatic Botany* 64:247–260.
- Saltonstall K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *PNAS* 99: 2445–2449.
- SPSS, Inc. 2000. SPSS 10.1 for Windows. Chicago, IL. 300 pp.
- Van der Toorn, J. 1972. Variability of *Phragmites communis* in relation to the environment. *Van Zee Tot Land* 48:1–122.
- Vretare, V., S.E.B. Weisner, J.A. Strand, and W. Granéli. 2001. Phenotypic plasticity in *Phragmites australis* as a functional response to water depth. *Aquatic Botany* 69:127–145.
- White, D.A. 1993. Vascular plant community development on mudflats in the Mississippi River delta, Louisiana, USA. *Aquatic Botany* 45:171–194.
- White, D.A., and D.P. Hauber. 1998. Plant communities of the Mississippi River delta: Consequences of geological and hydrological events over the past 200 years. Book of Abstracts p. 18. World Deltas Symposium, New Orleans, LA. 103 pp.
- Yamasaki, S., and I. Tange. 1981. Growth responses of *Zizania latifolia*, *Phragmites australis*, and *Miscanthus sacchariflorus* to varying salinity. *Aquatic Botany* 10:229–23.

The following are higher quality copies of Figures 3 to 5

