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Predicting performance for ecological restoration: a case study using *Spartina alterniflora*

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Abstract. The success of population-based ecological restoration relies on the growth and reproductive performance of selected donor materials, whether consisting of whole plants or seed. Accurately predicting performance requires an understanding of a variety of underlying processes, particularly gene flow and selection, which can be measured, at least in part, using surrogates such as neutral marker genetic distances and simple latitudinal effects. Here we apply a structural equation modeling approach to understanding and predicting performance in a widespread salt marsh grass, *Spartina alterniflora*, commonly used for ecological restoration throughout its native range in North America. We collected source materials from throughout this range, consisting of eight clones each from 23 populations, for transplantation to a common garden site in coastal Louisiana and monitored their performance. We modeled performance as a latent process described by multiple indicator variables (e.g., clone diameter, stem number) and estimated direct and indirect influences of geographic and genetic distances on performance. Genetic distances were determined by comparison of neutral molecular markers with those from a local population at the common garden site. Geographic distance metrics included dispersal distance (the minimum distance over water between donor and experimental sites) and latitude. Model results indicate direct effects of genetic distance and latitude on performance variation among the donor sites. Standardized effect strengths indicate that performance was roughly twice as sensitive to variation in genetic distance as to latitudinal variation. Dispersal distance had an indirect influence on performance through effects on genetic distance, indicating a typical pattern of genetic isolation by distance. Latitude also had an indirect effect on genetic distance through its linear relationship with dispersal distance. Three performance indicators had significant loadings on performance alone (mean clone diameter, mean number of stems, mean number of inflorescences), while the performance indicators mean stem height and mean stem width were also influenced by latitude. We suggest that dispersal distance and latitude should provide an adequate means of predicting performance in future *S. alterniflora* restorations and propose a maximum sampling distance of 300 km (holding latitude constant) to avoid the sampling of inappropriate ecotypes.

Key words: adaptive divergence; common garden; ecological restoration; geographic distance; isolation by distance; performance; population differentiation; Spartina alterniflora; *structural equation modeling*.

Introduction

Population biologists have recognized for decades that adaptive population divergence may play a pivotal role in the success of ecological restoration activities that rely on the transplantation of foreign genotypes to disturbed ecosystems (Montalvo et al. 1997, Hufford and Mazer 2003, Broadhurst et al. 2006). Although numerous reciprocal transplantation experiments have documented a tendency for plant populations to be most highly adapted to their local environmental conditions (reviewed in Linhart and Grant 1996, Schluter 2000, Geber and Griffen 2003, Leimu and Fischer 2008), the precise scale over which meaningful levels of divergence occur has rarely been determined (McKay et al. 2005; but see Galloway and Fenster 2000, Joshi et al. 2001, Becker et al. 2006, Raabová et al. 2007), and there is considerable doubt about the consistency of the relationship between local adaptation and geographic scale over the range of plant species studied (Leimu and Fischer 2008). Thus, a clear understanding of scale effects on transplant success may require a species-by-species approach, which will prove important in assuring not only that transplanted populations achieve self-sustainability over time, but also that the mean fitness of any preexisting populations in the local or regional area is maintained. The mixing of maladapted genes within an otherwise locally adapted gene pool (Burton et al. 1999, Edmands 1999, Montalvo and Ellstrand 2001, Hufford and Mazer 2003, Rice and Emery 2003, McKay et al. 2005) and/or the break-up of coadapted gene

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complexes (Donohue et al. 2000, Franks and Weis 2008) may severely limit sexual recruitment through outbreeding depression.

It is primarily the competing processes of selection and gene flow that affect adaptive population divergence (reviewed in Slatkin 1985, Kawecki and Ebert 2004). Whereas the direction, strength, and scale of selection pressures can be difficult to gauge in natural settings, gene flow is relatively straightforward to measure using any of a number of modern molecular technologies (reviewed in Neigel 1997, Ouborg et al. 1999). However, under strong selection regimes, gene flow estimates based on neutral DNA markers may tend to over- or underrepresent adaptive genetic variation related to performance indicators such as growth and fecundity (reviewed in Merilä and Crnokrak 2001, Reed and Frankham 2001, Lenormand 2002, McKay and Latta 2002; cf. Sambatti and Rice 2006). Understanding the degree to which neutral marker variation reflects adaptive population divergence is thus a necessary first step in developing molecular-marker-based tools for restoration (McKay et al. 2005). A useful second step involves determining the degree to which geographic distance effects, as a surrogate for regional-scale variation arising from selection, contribute to adaptive population divergence beyond that explained by simple gene flow (Galloway and Fenster 2000, Montalvo and Ellstrand 2000, Joshi et al. 2001; cf. Smith et al. 2005). Given the time and expense involved in marker-based assays, adaptive divergence could optimally be judged simply on the basis of geographic distance; however, there is a need to disentangle the relationships among genetic vs. geographic effects before meaningful conclusions can be drawn. For example, there is a good deal of evidence that gene flow varies depending on particular species traits (Hamrick and Godt 1990, Hamrick et al. 1991): widespread plant species that are outcrossing and rely on pollen dispersal by wind or seed dispersal by water may exhibit a much clearer relationship between geographic and genetic distance than primarily selfing and/or endemic species that rely on insect pollination (e.g., Raabová et al. 2007). In the former case, geographic distance is more likely to reflect genetic distance as it pertains to adaptive population divergence because pronounced local adaptation is less likely to develop.

In this study, we examine a geographically widespread saltmarsh grass (smooth cordgrass, *Spartina alterniflora*), whose seeds are dispersed over potentially large distances by water, to disentangle the relationships between adaptive population divergence, modeled as performance; gene flow, modeled as neutral marker genetic distance; and geographic distance, separated into independent measures of dispersal distance and latitudinal distance. With a native distribution extending from northern Mexico on the Gulf Coast to southern Canada on the Atlantic Coast, *S. alterniflora* is used extensively as a foundation species in salt marsh restoration, particularly in states such as Louisiana where subsidence and coastal erosion claim more than 65 km^2 of wetland per year (Dunbar et al. 1992). Marsh reclamation using sediments generated from dredging activities is an ongoing process in the northern Gulf of Mexico. In many instances, the active planting of *S. alterniflora* is conducted soon after marsh creation, although the issue of adaptive population divergence is rarely considered in the selection of donor materials. Rather, clones are chosen from a limited number of accessions based on their performance under controlled conditions (e.g., Harrison et al. 2001). In other instances, the active restoration process ends with marsh creation, and subsequent marsh development occurs via natural immigration from neighboring populations. Previous studies of the colonization dynamics of created sites in the Sabine National Wildlife Refuge of southwestern Louisiana have shown *S. alterniflora* to be one of the earliest and most aggressive colonizers (Proffitt and Young 1999, Edwards and Proffitt 2003, Proffitt et al. 2003), although due to the size (>100 ha) and relative rarity of tidal inundation of these sites, a span of 5–10 years is generally required for complete vegetative coverage to occur. Prior to this time, a unique opportunity exists for conducting a variety of planting experiments on uncolonized sediments under relatively natural conditions (e.g., Proffitt et al. 2003, 2005; C. E. Proffitt and S. E. Travis, *unpublished manuscript*).

We collected donor materials from 23 *S. alterniflora* populations spanning the northern Gulf of Mexico and Atlantic Coasts of the United States (Fig. 1) for transplantation to a common garden site and then measured performance over one entire growing season. Using a structural equation modeling (SEM) approach (Pugesek et al. 2003, Grace 2006), we assessed the combined effects of geographic distance and genetic distance on performance, which was modeled as a latent process described by multiple indicator variables. An SEM was used because of its suitability for addressing multivariate hypotheses about networks of relationships among interacting variables.

Hypothesized models relating geographic and genetic distance effects to performance

The modeling process in SEM is guided by the investigator's a priori and theoretical knowledge and begins with a consideration of hypothesized relationships based on mechanisms thought to operate in the system (Grace and Bollen 2008). There were four competing models we wished to evaluate in this study, all of which involved the relationship of plant performance to genetic distance, dispersal distance, and latitude (Fig. 2). We define dispersal distance in this study as the minimum distance that a seed would have to travel to disperse between sites, assuming waterborne dispersal (note that our calculations revealed a correlation of 0.985 between dispersal distances based on

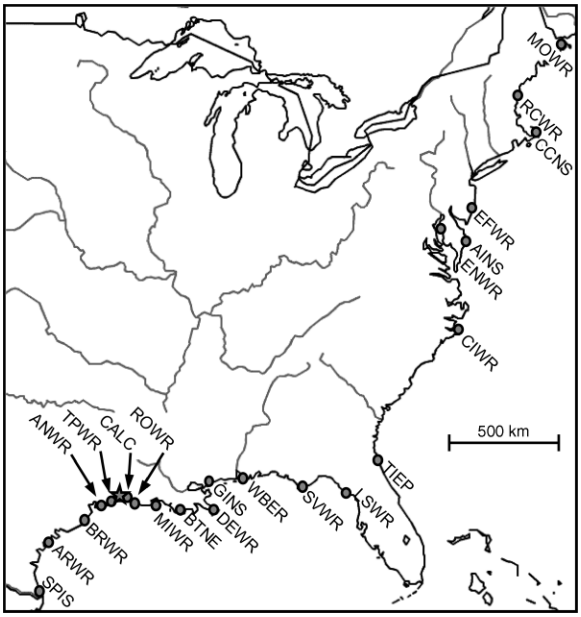

FIG. 1. A map of the Gulf of Mexico and Atlantic Coasts of North America showing the locations of 23 donor sites (shaded ovals) where *Spartina alterniflora* was collected for a common garden experiment on performance. The locations of the experimental site at the Sabine National Wildlife Refuge in southwestern Louisiana and of the nearest donor site (used as a reference site for calculating genetic distances) are denoted by the star. Site abbreviations, from bottom left to top right, are as follows: SPIS, South Padre Island, Texas; ARWR, Aransas National Wildlife Refuge, Texas; BRWR, Brazoria National Wildlife Refuge, Texas; ANWR, Anahuac National Wildlife Refuge, Texas; TPWR, Texas Point National Wildlife Refuge, Texas; CALC, Calcasieu Estuary, Louisiana; ROWR, Rockefeller State Wildlife Refuge, Louisiana; MIWR, Marsh Island State Wildlife Refuge, Louisiana; BTNE, Barataria-Terrebonne National Estuary, Louisiana; DEWR, Delta National Wildlife Refuge, Louisiana; GINS, Gulf Islands National Seashore, Mississippi; WBER, Weeks Bay National Estuarine Research Reserve, Alabama; SVWR, St. Vincent National Wildlife Refuge, Florida; LSWR, Lower Suwannee National Wildlife Refuge, Florida; TIEP, Timucuan Ecological and Historic Preserve, Florida; CIWR, Cedar Island National Wildlife Refuge, North Carolina; ENWR, Eastern Neck National Wildlife Refuge, Maryland; AINS, Assateague Island National Seashore, Virginia; EFWR, Edwin B. Forsythe National Wildlife Refuge, New Jersey; CCNS, Cape Cod National Seashore, Massachusetts; RCWR, Rachel Carson National Wildlife Refuge, Maine; MOWR, Moosehorn National Wildlife Refuge, Maine.

waterborne dispersal and simple linear distances between sites, so relative values would not appreciably differ between these two approaches). In all four models we expected a direct effect of genetic distance on performance, which assumes that local selection pressures are not so extreme as to disconnect neutral marker variation from quantitative genetic variation. (Note that in this paper we follow the standard convention of referring to direct and indirect pathways in the models as direct and indirect effects.) We expected that regional-scale selection pressures would likely be reflected to some extent by latitudinal variation in climatic variables such as temperature and solar radiation (Vogel et al. 2005) and thus expected that latitude would explain a significant amount of performance variation beyond that explained by gene flow (see Santamaria et al. [2003] and Becker et al. [2006] for examples of latitudinal effects on performance in other plant species). Based on numerous molecular-marker-based studies, including previous studies of *S. alterniflora* conducted over a much more limited geographical range (Travis et al. 2002, Travis and Hester 2005), we hypothesized a positive effect of dispersal distance on genetic distance, i.e., genetic isolation by distance. The model shown in Fig. 2 minus paths b and c represents the "basic" model described by these common assumptions.

We further allowed for the possibility of a direct effect of latitude on genetic distance (Fig. 2) beyond its indirect influence mediated through its linear relationship with dispersal distance. This might be expected if, for example, latitudinal distance was more limiting to gene flow than longitudinal distance (a very real possibility). We also allowed for the possibility of a direct effect of dispersal distance on performance (path b) unrelated to its indirect effect through its relationship with genetic distance, which could result from there being a longitudinal gradient in an unmeasured environmental variable or some other disconnect between dispersal distance and genetic adaptation, perhaps owing to microscale selection factors. Our final, or "full" model, included both paths b and c.

A second step in the modeling process, following the description of general hypotheses, is the "specification" of structural equation models (SE models). In this step, theoretical ideas (summarized in Fig. 2) are translated

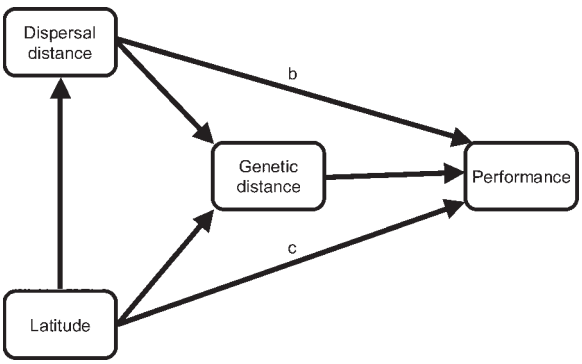

FIG. 2. A conceptual model depicting hypothesized relationships between geographic distance effects, genetic distance (as gauged by neutral DNA markers), and plant performance in *Spartina alterniflora*. Four competing models are contained in this figure. The basic model includes all paths not labeled with a letter, whereas model B considers, in addition to the paths included in the basic model, the possibility of a direct effect of dispersal distance on performance unrelated to genetic distance. Model C adds to the basic model by considering the possibility that latitude exerts a direct effect on genetic distance unrelated to dispersal distance, while the full model includes all paths from the basic model plus models B and C.

PLATE 1. A photograph of the experimental site located in the Sabine National Wildlife Refuge (southwestern Louisiana, USA), taken approximately one year following site creation, and two years prior to experimental setup. The small clumps of vegetation appearing in the photo are naturally colonizing *Spartina alterniflora*. Photo credit: C. E. Proffitt.

into statistical model form. This translation is determined in part by the data that are available to serve as measures or "indicators" for the conceptual entities of interest (performance, genetic distance, dispersal distance, and latitude). In this case, performance was modeled as a latent factor characterized by multiple responses. In our study, we measured 12 possible indicators of performance, ranging from physiological to growth to reproductive indicators. For the other three concepts, single indicators were available and considered suitable measures for each.

In order to maximize the relevance of our results to the resource management community, we posed four specific questions in relation to our SE model. (1) Which of the 12 chosen indicators of performance best describe variation among the donor sites? (2) To what extent does genetic distance, gauged on the basis of neutral molecular markers, reflect adaptive variation affecting the performance of transplants? (3) Do other predictors, including dispersal distance and latitude, explain additional performance variation unaccounted for by genetic distance? (4) In the absence of genetic information, how well do geographic distance metrics predict variation in performance? The goal of our analysis, therefore, was to evaluate modeling results so as to ascertain the answers to these questions.

METHODS

We collected live plant material for our common garden experiment during the fall of 2002. Among our 23 collection sites, each representative of native *S. alterniflora* marsh, we chose a greater number from the Gulf Coast than from the Atlantic region because we assumed that the ability of the transplants to grow and reproduce at the experimental site would decline fairly rapidly with distance from the donor site. To insure that an adequate representation of plant genotypes was sampled from each donor site, we sampled plant materials from eight separate points separated by at least 40 m. Plant materials, hereinafter referred to as donor clones, were sampled haphazardly with respect to any existing environmental heterogeneity at each donor site. Each donor clone consisted of an uprooted soil plug encompassing at least eight ramets, together with attached roots and rhizomes. Clones were planted in separate ~3.8-L pots with a surrounding soil mixture of equal parts silt (Mississippi River silt) and commercial potting soil and were allowed to grow in 3 ppt seawater. We acclimated all donor clones over the winter in a greenhouse in Lafayette, Louisiana, USA, located ~140 km east–northeast of the experimental site, prior to planting them in the field in April of 2003.

The experimental site consisted of a large (>200 ha) mudflat created from dredged sediment by the U.S. Army Corps of Engineers in the fall of 1999 in an ongoing effort to restore functional wetlands to the Sabine National Wildlife Refuge (see Plate 1). The site, located at 29°54′35″ N, 93°22′50″ W, exhibited a very slight slope, with open water along one edge; therefore, donor clones were planted in a randomized block design, with the blocks intended to factor out potential elevational effects. Each block consisted of one clone from each of the 23 donor sites randomly assigned to a location within a line running at right angles to the elevational gradient. Adjacent clones in a row were separated by 5 m, with 10 m of separation between adjacent rows or blocks. Thus, the overall design included eight rows of 23 clones each. Individual donor clones were planted in the field as groups of 10 ramets after being mechanically separated from the remainder of each potted clone in the greenhouse.

We measured the following performance characteristics of each donor clone at the end of a single growing season lasting approximately six months: survival (as a binary variable); total number of stems; clone diameter (averaged between two measurements taken on north–south and east–west axes); stem density (number per square meter); mean stem height (measured to the top of the tallest leaf), width (measured at ground level), and height × width; sum of stem heights, widths, and heights × widths; and number of inflorescences. At the peak of the first growing season (four months post-planting), photosynthetic rates were measured for each clone in microliters of O_2 per square meter per second using a LI-6400 portable photosynthesis system (LI-COR, Lincoln, Nebraska, USA).

We used molecular fingerprinting to assess the magnitude of genetic differentiation between the donor population lying nearest to the experimental site, which was located across a narrow canal and which has served us repeatedly as a natural reference site in our previous work (Travis et al. 2002, 2004, Travis and Hester 2005), and all other donor populations, under the assumption that this population should be genetically predisposed to growing well under local environmental conditions. We extracted DNA from a small amount (~1 g) of leaf tissue collected from each clone using a cetyltrimethylammonium bromide (CTAB)-based method (Travis et al. 2002), and genotyped it using amplified fragment length polymorphisms (AFLPs) according to the methods of Travis and Hester (2005). We used a single, highly informative primer combination for our genotyping activities, which contained the selective nucleotides *Eco*RI-ACG and *Mse*I-AGT. This primer pair produced 37 polymorphic markers for distinguishing among populations. Population differentiation was computed as θ, an analog of Wright's F_{ST}, hereinafter referred to simply as F. This statistic was calculated using the Bayesian method of Holsinger et al. (2002), which compensates for the inability of dominant markers such as AFLPs to detect inbreeding.

Structural equation modeling was conducted using a two-stage approach, first developing a measurement model for the latent factor plant performance and then evaluating the network of influences on performance. Indicators for the performance factor were evaluated based on logical and numerical criteria. First, mortality variables were dropped from consideration to avoid mixing dichotomous and continuous variables in the factor model (and also because dichotomous variables contain less information). Second, measures of photosynthetic rates were observed to be more variable than other indicators and it was decided that these instantaneous measures contained a greater degree of measurement error than more integrative variables related to growth; thus, they were dropped from consideration. A confirmatory factor analysis was performed to determine whether the remaining 10 variables were all consistent with a single-factor model. The analysis was performed using the Amos 7.0 software for structural equation modeling (SPSS 2007). Model selection procedures were used to purify the factor model and retain only those indicators showing strongly consistent responses (DeVellis 2003). Once that was accomplished, evaluations of full structural equation models (including latitude, dispersal distance, genetic distance, and performance indicators) were conducted using the methods for model evaluation described in Grace (2006: chapter 5). Briefly, these methods are based on testing the hypothesized models rather than null hypothesis testing. The goal in this process is to obtain a model that is consistent with the data based on comparisons between the covariances in the data and those implied by the model. Model adequacy is indicated by test statistics (e.g., chi-square tests) that show nonsignificant differences between observed and model-implied covariances (P values >0.05 indicate no significant deviations between model and data). Also, models are selected that are parsimonious, and pathways that fail to contribute to data explanation are excluded.

Results

The measurement model for the latent factor plant performance retained five of the 12 indicators available. The remaining indicators were omitted because they failed to show high and balanced loadings on a common factor and their inclusion resulted in significant deviations ($P < 0.05$) from a one-factor model. The retained indicators, in descending order relative to their loadings on performance, were mean clone diameter, mean number of stems per clone, mean number of inflorescences per clone, mean stem height, and mean stem width. The latent variable performance, by itself, explained 73–95% of the variation in the top three indicators.

All of the bivariate relationships between the five indicators retained in the model and each of the three

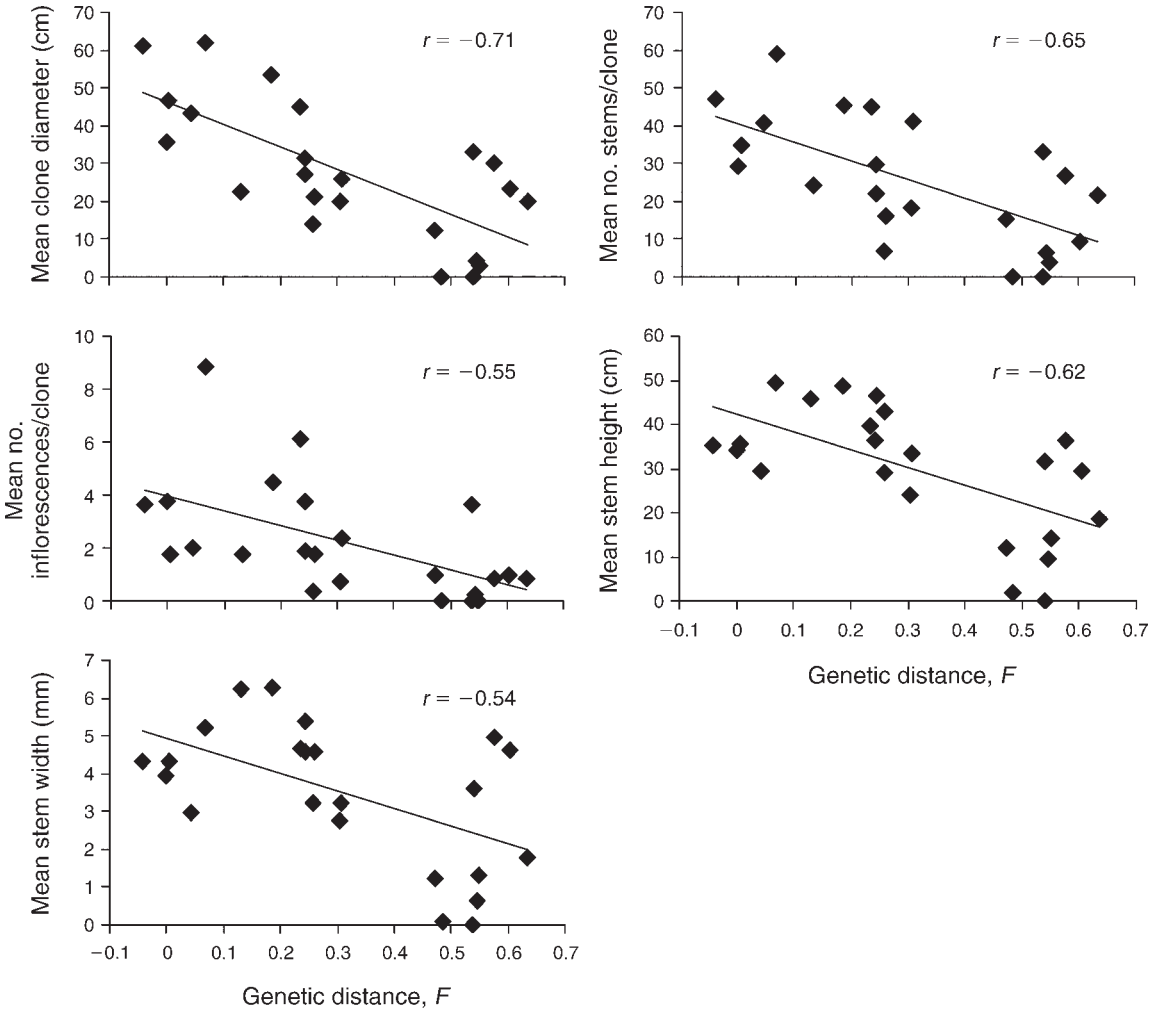

FIG. 3. Bivariate relationships of genetic distance with five indicators determined from a structural equation model to have significant loadings on performance in *Spartina alterniflora*. Note that slightly negative genetic distance estimates should be interpreted as zeroes.

predictor variables (Figs. 3–5) were negative and significant at $P < 0.01$ (P values are not shown), with the exception of the relationship between number of inflorescences and latitude ($P = 0.056$). The bivariate relationships between each of the performance indicators and genetic distance were linear, with the highest correlations pertaining to clone diameters ($r = -0.71$) and numbers of stems ($r = -0.65$; Fig. 3). The highest correlations seen among the bivariate relationships involving the two geographical distance effects pertained to stem heights and widths, although these relationships were consistently linear for dispersal distance ($r = -0.84$ and -0.79 for stem heights and widths, respectively; Fig. 4), whereas they were quadratic for latitude ($r = -0.86$ and -0.84; Fig. 5). The nonlinear relationships between the performance indicators and latitude were characteristically flat over the range of latitudes represented by the 15 Gulf Coast sites, although the two lowest latitude sites played a highly influential role in this relationship, whereas they were negative over the northward progression of sites extending up the Atlantic Coast (Fig. 5). Several correlations existed among the indicators themselves beyond what was explained by their mutual association with plant performance as a latent factor. Stem width was positively correlated with stem height ($r = 0.91$), as well as with clone diameter ($r = 0.36$).

A comparison of our basic model with several more complex models (Fig. 2) indicated that the basic model provided a good fit to the data (as indicated by a nonsignificant P value for the model chi-square test). The basic model was also found to be the most parsimonious model, with paths b and c found to be unnecessary to explain the data. Chi-square values for the three models that provided a reasonable fit to the data (basic, B, C) were 32.09 (df = 26, $P = 0.19$), 31.88 (df = 25, $P = 0.16$), and 32.03 (df = 25, $P = 0.16$). Single-degree-of-freedom chi-square tests indicated that neither pathway b nor pathway c significantly improved the

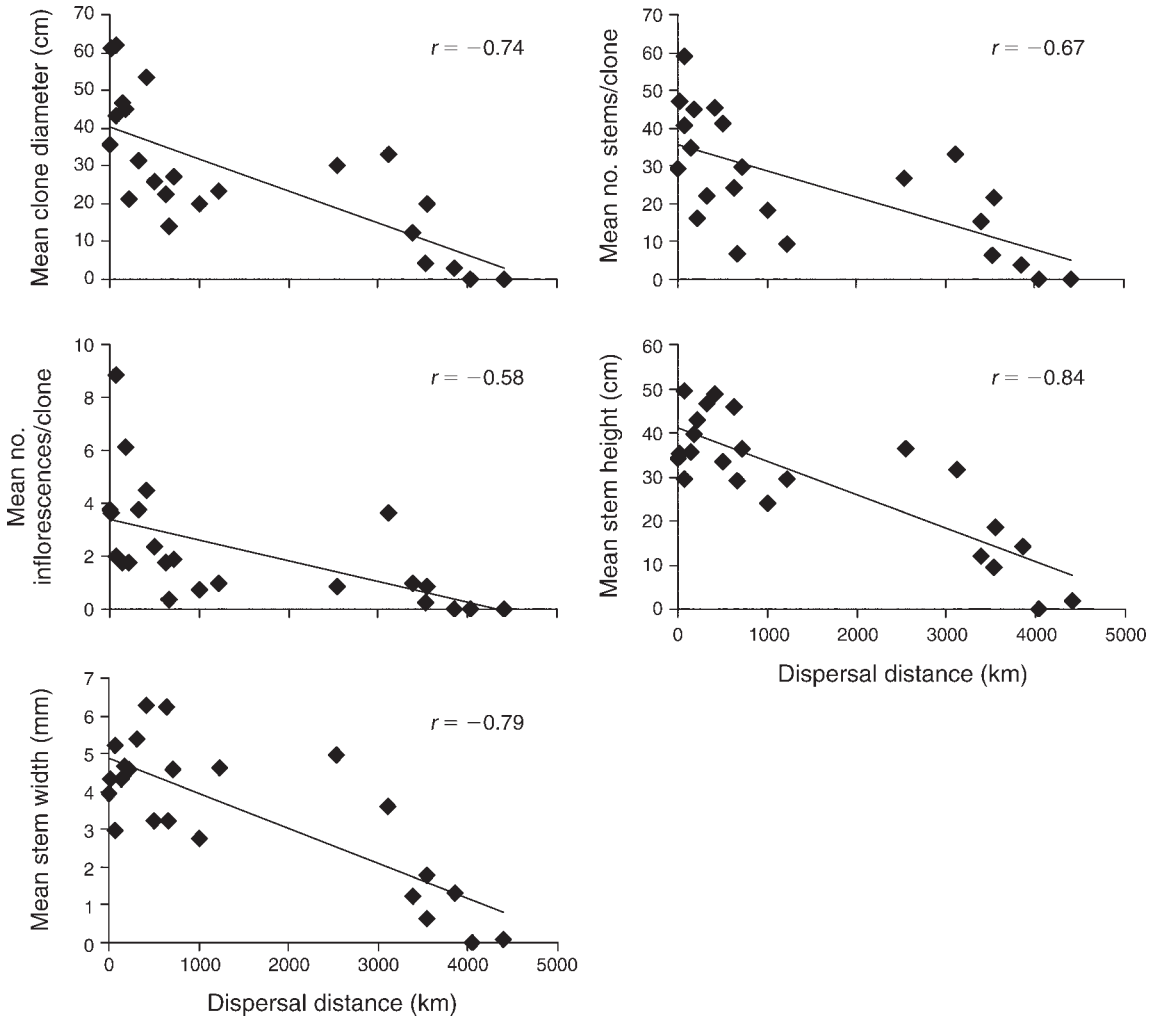

FIG. 4. Bivariate relationships of dispersal distance with five indicators determined from a structural equation model to have significant loadings on performance in *Spartina alterniflora*.

model. Comparison of models using other indices also supported the conclusion that the basic model was the most defensible of the models. Thus, we selected the basic model for drawing inferences.

The basic model (Fig. 6) contained direct effects of genetic distance and latitude on performance, whereas dispersal distance was directly affected by latitude and exerted an indirect effect on performance through its direct effect on genetic distance. Genetic distance and latitude together explained 68% of the variation in performance. However, genetic distance exhibited approximately twice the predictive power of latitude based on standardized path coefficients (0.86 vs. −0.41), indicating that population divergence, judged on the basis of neutral molecular markers, is highly consistent with adaptive population divergence in *S. alterniflora*. Not surprisingly, given the observed bivariate relationships between each of the performance indicators and genetic distance on the one hand vs. latitude on the other, genetic distance had a linear effect on performance, whereas latitude had a quadratic effect (both first- and second-order terms for latitude contributed to variance explanation). Latitude also had a direct effect on two of the five performance indicators, mean stem height and width, suggesting that *S. alterniflora* is genetically predisposed to variable stem morphology, depending on latitude. In fact, latitude alone was the stronger predictor of both stem height and width based on standardized path coefficients: stem height was represented by path coefficients of 0.40 and −0.58 representing performance vs. latitude, respectively, while stem width was represented by path coefficients of 0.30 and −0.61 for these same effects. Together, the latent factor performance and the observed variable latitude explained 80% and 69% of the variation in stem heights and widths, respectively.

Genetic isolation by distance was strongly indicated by the final SE model (Fig. 6), with dispersal distance

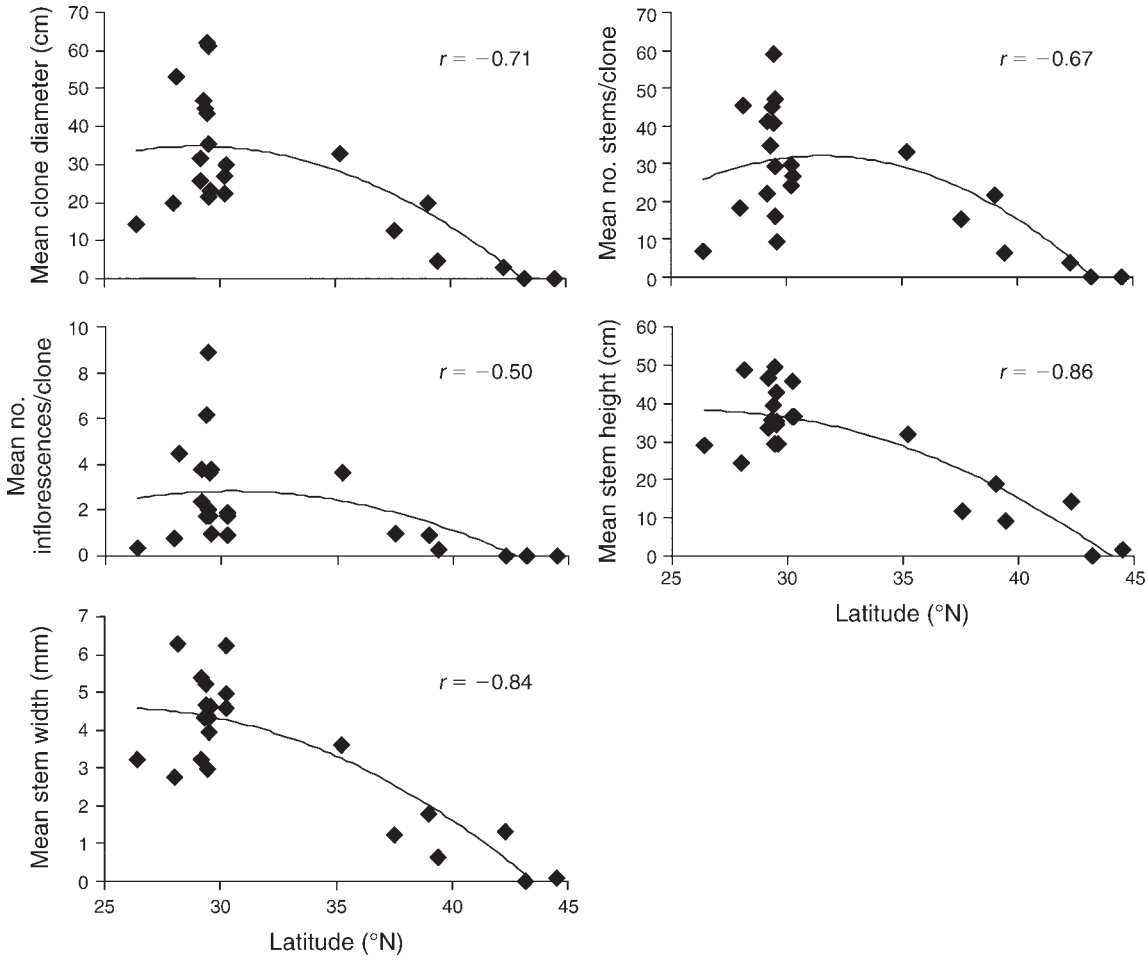

FIG. 5. Bivariate relationships of latitude with five indicators determined from a structural equation model to have significant loadings on performance in *Spartina alterniflora*.

explaining 58% of the variation in genetic distance. This relationship was significantly curvilinear (both first- and second-order terms contributed to the explanation of variance), with genetic distance rising sharply with dispersal distances spanning ~1200 km and then leveling off (Fig. 7). As hypothesized, latitude explained a large proportion, 85%, of the variation in dispersal distance via a strictly linear relationship. Thus, model results indicate that latitude had both a direct effect on performance as well an indirect affect through its relationship with dispersal distance, which in turn affected performance indirectly through its relationship with genetic distance. Not surprisingly, given the quadratic nature of the relationship between dispersal distance and genetic distance, the bivariate relationship between latitude and genetic distance was also quadratic (Fig. 7). Overall, the ability of the model to predict performance in the absence of information on genetic distances would not be reduced (based on reduced-form model runs: $\chi^2 = 16.56$, df = 18, $P = 0.55$). Thus, it is still possible for variation in performance to be predicted strictly on the basis of dispersal distance and latitude.

DISCUSSION

The basic model (the one selected as our best model) included a direct effect of both genetic distance, as gauged by neutral molecular markers, and latitude on performance. Dispersal distance, measured as the minimum distance over water between donor and experimental sites, exerted only an indirect effect on performance by contributing to genetic isolation by distance. Latitude also exerted an indirect effect on genetic distance through its monotonic effect on dispersal distance and therefore had both direct and indirect influences on performance. In total, these three factors explained 68% of the variation in performance among the 23 donor sites, with genetic distance representing the single most effective predictor. However, in the absence of information on genetic distances, the simple measures of dispersal distance and latitude serve as reasonable substitutes for predicting the performance of potential source materials for restoration, together explaining 58% of the variation in performance.

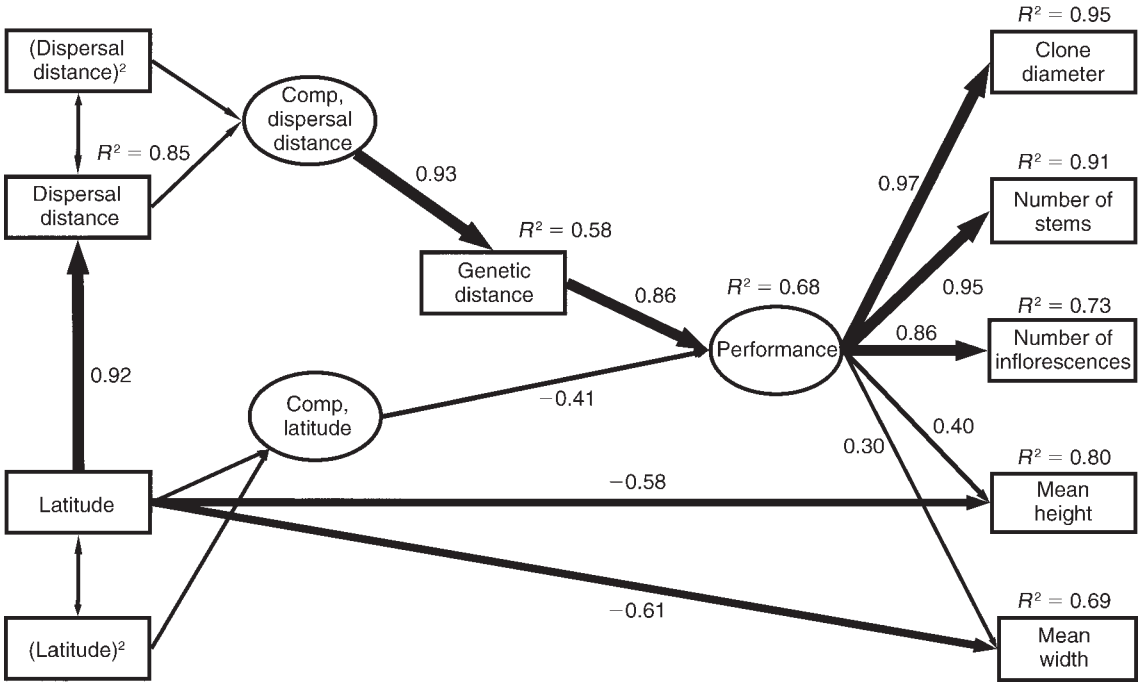

FIG. 6. Results for the final model ($\chi^2 = 32.1$, df = 26, $P = 0.19$). Circles represent latent variables, whereas boxes represent observed variables. Arrow widths reflect the overall explanatory power of significant relationships, with the exception of the arrows depicting composite effects (labeled as "Comp"), which combined each geographic distance metric with its respective squared values to reflect quadratic effects. Standardized path coefficients accompany arrows when multiple paths intersect with a particular variable; otherwise, numbers accompanying arrows are simply loadings.

In order to unravel the relationships between genetic distance, geographic distance, and performance, we used an SEM approach, which provided the means for testing multivariate hypotheses and for partitioning relationships among multiple pathways. A traditional multiple regression approach would have required us to either perform separate regressions for each response variable or simply select one for inference, resulting in a substantial loss of information and generality. By allowing us to explicitly consider causal chains of relationships, SEM also provided a framework for evaluating alternative predictive models as well as for detecting unanticipated effects.

The value of our SEM approach can also be gauged in terms of its capacity for allowing us to model performance as a latent process, with each of the measured responses reflecting performance to varying degrees. Of the five responses serving as indicators for performance, mean clone diameter had the highest loading at 0.97 (Fig. 6). Thus, this indicator could be considered the single most effective measure of performance for the purpose of selecting donor materials for marsh restoration in the future. Among the residual correlations we detected, we noted a positive scaling relationship between mean stem height and mean stem width. More interestingly, we found a residual correlation between stem width and clone diameter, perhaps

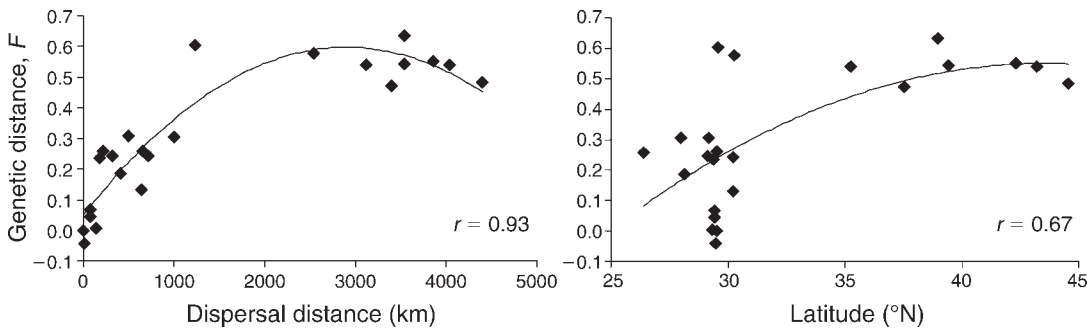

FIG. 7. Bivariate relationships of genetic distance with two measures of geographic distance (dispersal distance and latitude), in *Spartina alterniflora*. Note that slightly negative genetic distance estimates should be interpreted as zeroes.

indicating that basal stem diameter provides a quantitative measure of underground nutrient reserves needed for lateral clone growth.

Because our study was geared toward broad-scale restoration practices that provide better information, our primary interest was in how transplanted materials perform in disturbed sites where no preexisting population exists. Thus, we adopted a common garden approach designed to evaluate broad-scale effects such as genetic and geographic distance on performance. Notably, this approach suggests several caveats. First, it cannot provide a true test of local adaptation because it does not allow for the sort of "home site advantage" typically sought in reciprocal transplantation studies (reviewed in Kawecki and Ebert 2004, Leimu and Fischer 2008). In our case, a reciprocal transplantation approach would have greatly limited our ability to quantify distance effects among a large number of donor populations distributed over a broad geographic area and so was intentionally avoided. Second, our approach did not allow us to focus on adaptive divergence resulting from specific selection pressures that might be expected to vary on a local scale. Previous research has indicated the importance of micro-scale effects on local adaptation in *S. alterniflora* and on salt marsh plants in general (Seliskar 1985, Bertness and Ellison 1987, Gallagher et al. 1988, Richards et al. 2004, 2005). While we were unable to consider these effects in our study, it seems likely that they were largely responsible for the fairly high degree of scatter we observed when plotting geographic and genetic distance against performance (Figs. 3–5). In spite of the fact that 68% of the variation in performance among donor sites could be explained based on broad-scale factors such as latitude, much of this explanatory power was lost at <5 degrees of separation. At these distances, where major climatic gradients in temperature and solar radiation are less pronounced, other environmental factors such as soil type and tidal flushing may assume an overriding importance. Future work should attempt to include such variables in order to adequately characterize selection pressures acting on a local scale, particularly across the northern Gulf of Mexico Coast where latitudinal variation is limited. In addition, the ages of the donor populations should be considered, since some plant species have been shown to harbor varying magnitudes of mutational load depending on population age (e.g., Paland and Schmid 2003).

Due to unavoidable practical constraints, our statistical analysis was limited to data collected over the course of a single growing season, whereas several reciprocal transplant experiments that have considered time as a factor have indicated that patterns of adaptive divergence may not be temporally consistent (e.g., Rice and Mack 1991, van Tienderen and van der Toorn 1991, Jordan 1992, Galloway and Fenster 2000, Becker et al. 2006, Raabová et al. 2007, Wright 2007, Hereford and Winn 2008) or may take several years to develop (Becker et al. 2006). It is worth noting that we continued to collect data from our experimental plot during a second growing season. We chose not to formally present this data because >10% of our experimental clones lying along the periphery of the study plot had been overtaken by encroachment from naturally colonizing clones by the middle of the second season. However, this second season provided us with a sufficient amount of data to check for consistency between seasons, and similar trends in growth and reproduction were observed. Not surprisingly, several other studies have indicated that plant size as an indicator of performance during the first year of establishment is highly correlated with subsequent size measurements (Montalvo 1994, Montalvo and Ellstrand 2000).

We chose to use transplanted clones for our experiment rather than seeds in spite of observations by other researchers that selection on fitness parameters is often most pronounced during the seedling stage (e.g., Antonovics and Primack 1982, van Tienderen and van der Toorn 1991, Nagy and Rice 1997, Keller and Kollmann 1999, Galloway and Fenster 2000, Bischoff et al. 2006*a*, Raabová et al. 2007). We focused on clones rather than seeds for several reasons. Perhaps most importantly, although some attempts have been made to aerially broadcast seed for *S. alterniflora* restoration, seed viability tends to be limited in this species (Hartman 1988, Daehler and Strong 1994), and the majority of restorations have therefore been carried out using cloned materials. Thus, our use of clones was both more realistic from a restoration standpoint and more likely to yield a sufficient quantity of data for sound statistical inference. In addition, our focus on clones rather than seeds allowed us to avoid possible maternal affects. Unfortunately, it may also have heightened the role of selection acting on seedling genotypes in creating substantial levels of local adaptation of clones to their home sites. If both maternal effects and home-site selection on seedling genotypes are to be avoided in the future, it will be necessary to sexually propagate seed under controlled conditions for several generations prior to undertaking experiments (cf. Galloway and Fenster 2000).

Management implications

Overall, our results suggest that the performance of *S. alterniflora* can reasonably be gauged on the basis of geographic distance and that this species is to a large extent adapted on a regional scale, as donor materials taken from >300 km away performed as well as local populations in our common garden experiment. Similar results have been observed in other widespread plant species used for restoration (e.g., Galloway and Fenster 2000, Joshi et al. 2001, Becker et al. 2006, Ellis et al. 2007) and suggest that distance-based limitation of gene flow plays a major role in creating adaptive divergence in these species. In spite of our findings, it would be imprudent to conclude that any single donor site within

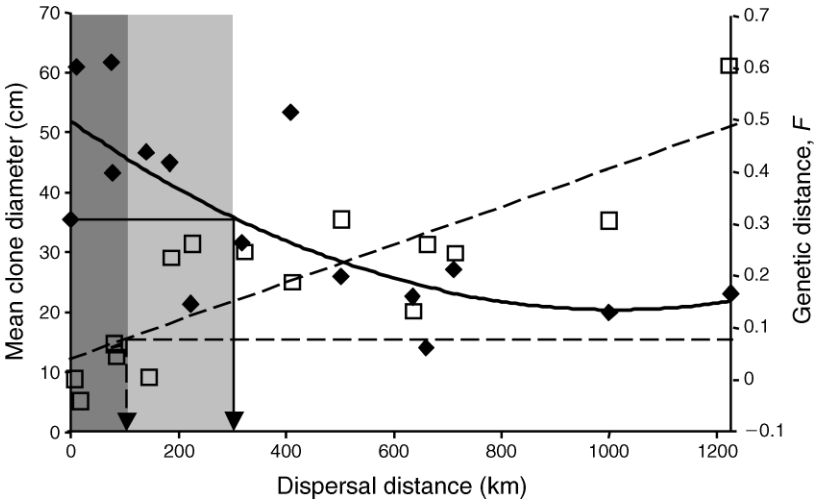

FIG. 8. A plot of the relationship between dispersal distances encompassing the Gulf Coast, mean clone diameter (solid line, solid diamonds), which was the indicator variable with the highest loading on performance, and genetic distance (dashed line, open squares; note that slightly negative genetic distance estimates should be interpreted as zeroes). The dashed arrow and the corresponding dark gray range of dispersal distances represent the range within which epitypes might be expected to occur, whereas the solid arrow and the corresponding light gray range of dispersal distances represent the range within which ecotypes might be expected to occur.

a certain minimum distance of a proposed restoration site would be an adequate source of plant materials by itself, since we observed a good deal of unexplained scatter in mean performance among our donor sites, likely as a manifestation of undescribed local environmental selection pressures. In fact, if we focus on our single best predictor of performance, mean clone diameter, we see that the most local population in our experiment, located within several hundred meters of our restoration site, was outperformed by five other populations located at distances of up to 180 km (Fig. 8). This would seem to defy the existence of a home site advantage in *S. alterniflora*, although given the nature of our experiment we had no true home site, and at any rate, a home site advantage has been found to be far from universal in studies of local adaptation (e.g., Crespi 2000, Bischoff et al. 2006*b*, Leimu and Fischer 2008). We would suggest collecting donor materials from multiple sites within a distance dictated by the regression of performance, e.g., mean clone diameter, on dispersal distance, using the predicted distance at which mean clone diameter comes to equal that of the most local site in our experiment, which occurs at ~300 km (Fig. 8). In order to improve the level of performance and to guarantee adequate levels of genetic diversity (we have dealt with the importance of genetic and genotypic diversity in *S. alterniflora* restoration elsewhere; Travis et al. 2002, 2004, Proffitt et al. 2003, 2005, Travis and Hester 2005), we would suggest collecting from at least three sites within the prescribed distance (McKay et al. 2005) and collecting across the full range of microenvironmental conditions existing within each site. This may not be a perfect solution, particularly since we cannot be certain that the trends we observed would hold true for other restoration sites, particularly those lying along the Atlantic Coast, but it should provide a good first approximation.

Finally, it should be noted that our discussion thus far has assumed that the performance variation we observed in *S. alterniflora* is strictly ecotypic in nature, without considering the possibility that similar ecotypes may nevertheless exhibit differences in the genetic architecture underlying their adaptive traits. One of the mechanisms for outbreeding depression is the breakdown of co-adapted gene complexes that results when previously isolated populations are crossed, even if these populations represent similar ecotypes (Montalvo and Ellstrand 2001). Hufford and Mazer (2003) termed populations that are both adaptively and genetically similar "epitypes," and we can use our regression of genetic distance on dispersal distance to predict the maximum distance at which epitypes should occur in *S. alterniflora* (Fig. 8). This is based on Wright's (1978) recommended range of genetic distances representing low-to-moderate levels of genetic differentiation. If we conservatively apply a cut-off at $F = 0.08$, then we would conclude that it would be desirable for donor materials to be collected at distances of no greater than ~100 km from a proposed restoration site. Such a limited distance may seem somewhat extreme to resource managers, but given the overall abundance of *S. alterniflora* throughout most of its native range, the task of collecting plant materials within this distance should not prove particularly difficult and is well in keeping with the time-honored tenet that calls for restoration activities to be conducted using the most local materials available (Jones et al. 2001, Vergeer et al. 2003, Walker et al. 2004).

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