Final report to the U.S. Fish and Wildlife Service:

Spread and genetic relatedness of native vs. introduced *Phragmites australis* in Utah wetlands

Karin M. Kettenring[1]* and Karen E. Mock[2]

[1]Ecology Center and Dept. of Watershed Sciences, Utah State University, Logan, UT 84322
[2]Ecology Center and Dept. of Wildland Resources, Utah State University, Logan, UT 84322
*author for correspondence: karin.kettenring@usu.edu; 435.797.2546

Executive Summary

Utah is experiencing a dramatic invasion of an aggressive European subspecies of the common reed (*Phragmites australis* subsp. *australis*). This invasion is threatening recreation resources, wildlife habitat, and native wetland ecosystems. In this study, we used genetic tools to determine how, and to what extent, introduced *Phragmites* is spreading among major Utah wetlands. We also assessed native *Phragmites* (*Phragmites australis* subsp. *americanus*) spread to put our introduced *Phragmites* results in context. In addition, we determined if native *Phragmites* is being replaced by introduced *Phragmites* and if the two subspecies are hybridizing. Our results indicate that introduced *Phragmites* is effectively reproducing and dispersing through both rhizomes and seed but compared with native *Phragmites*, seems to be spreading largely by seed. Also, we found that levels of gene flow among Utah wetlands is quite high for introduced *Phragmites*, especially compared with the limited gene flow we found among native *Phragmites* populations. We found no evidence that native and introduced *Phragmites* are hybridizing, even where they coexist. In most locations, native *Phragmites* is not being replaced by introduced *Phragmites*. However, at Utah Lake, both subspecies co-occur and native *Phragmites* may be replaced by introduced *Phragmites* if it is not already. Based on our findings we recommend: (1) that control and prevention efforts for introduced *Phragmites* should target both forms of dispersal but focus on seeds and (2) that managers carefully monitor locations like Utah Lake, where the two subspecies are co-occurring, to prevent loss of native to introduced *Phragmites*.

Background

Phragmites australis subsp. *americanus* (common reed) is a plant native to wetlands of North America (Saltonstall *et al.* 2004). However, an aggressive European subspecies of *Phragmites* (*P. australis* subsp. *australis*) was recently identified and is considered to be invasive in wetlands across North America, including Utah (Saltonstall 2002). Introduced, invasive *Phragmites* is undesirable because it crowds out native vegetation, which provides habitat and food for many wildlife species. In the late 1980s in Utah, introduced *Phragmites* spread at a rapid rate with the retreat of the Great Salt Lake after historic floods and is now widespread in the wetlands of Bear Lake, Great Salt Lake, and Utah Lake, and along roadsides and in ditches throughout northern Utah (Kulmatiski *et al. In press*). Today, this plant is considered so problematic that the Utah legislature and Utah Division of Wildlife Resources (UDWR) have committed significant funding for large-scale *Phragmites* control efforts over the next decade. Under the guidance of Randy Berger (UDWR), thousands of acres of *Phragmites* are being sprayed to control this invasive plant on state lands, in addition to various control efforts in other areas like the U.S. Fish and Wildlife Service's Bear River Migratory Bird Refuge.

Despite widespread control efforts of introduced *Phragmites* in Utah and elsewhere, we still lack the basic information necessary to ensure that these efforts will be successful. For instance, we do not know how introduced *Phragmites* spreads (by seeds or rhizomes) within and among populations. Understanding how *Phragmites* spreads is important for prioritizing sites for control efforts and for determining whether control efforts need to be timed around seed production. Currently, *Phragmites* is sprayed in the fall following seed production. If seeds are an important means of dispersal, alternative methods may need to be developed to control this plant earlier in the growing season and limit further spread by seed. Alternatively, if *Phragmites* is spreading largely by rhizomes, control efforts will need to minimize soil disturbances (like disking) to limit its spread. Previous studies have shown substantial spread by seed of *Phragmites* in the Chesapeake Bay (McCormick *et al.* 2010, *In press*) but such a phenomenon has not been evaluated for introduced *Phragmites* in the West. The common perception in Utah is that *Phragmites* largely spreads by rhizomes. This work was undertaken to provide basic information to managers charged with controlling introduced *Phragmites* in Northern Utah.

Because native and introduced *Phragmites* both occur in Utah there is concern about whether native *Phragmites* is being replaced by introduced *Phragmites*. Because native *Phragmites* is much less aggressive than introduced *Phragmites* and provides important habitat for wildlife, its loss to introduced *Phragmites* is considered undesirable. Furthermore, there is concern that these two subspecies may hybridize, a phenomenon that could potentially lead to an even more aggressive plant than the current introduced *Phragmites*, as has occurred with cattails (*Typha* spp.; Galatowitsch *et al.* 1999). Native and introduced *Phragmites* have successfully hybridized under greenhouse settings, but thus far naturally-occurring hybrids have not been found in North America (Meyerson *et al.* 2010). In Utah, in areas where the two subspecies co-occur, there is concern that hybridization may be happening.

The main goals of our research were to determine:

(1) the extent of rhizome vs. seed dispersal in introduced vs. native *Phragmites*
(2) the extent of gene flow among populations of introduced vs. native *Phragmites*
(3) if hybridization between native and introduced *Phragmites* is occurring
(4) if introduced *Phragmites* is replacing native *Phragmites*

Assessment of seed vs. rhizome reproduction

Native and introduced *Phragmites* are capable of reproducing sexually through seed production or asexually through extension or fragmentation of lateral shoot segments (rhizomes). If the spread of native or introduced *Phragmites* is primarily through seed production, one would expect that stands would be genetically diverse, that genotypes would reflect random association of alleles at different loci and among different individuals (i.e. genotypic equilibrium and Hardy-Weinberg equilibrium), and that groups of individuals would show a pattern of increasing genetic differentiation with increasing geographic distance. Alternatively, if the spread of *Phragmites* is primarily through rhizome expansion and fragmentation, one would expect to find genetically identical groups of stems covering large spatial areas within and among stands. These identical groups, or "clones" may be contiguous or fragmented. Further, one would not expect to see the signatures of sexual reproduction (genotypic diversity, genotypic equilibrium, Hardy-Weinberg equilibrium, and differentiation with distance). Seed reproduction may be limited by seed inviability, reduced fertility (resulting from differing ploidy levels in parents), or by unfavorable habitats or climates (McKee and Richards 1996; Wijte and Gallagher 1996; Ishii and Kadono 2002; Greenwood and MacFarlane 2006; Saltonstall and Stevenson 2007; Kettenring and Whigham 2009; Kettenring *et al.* 2010). Rhizome reproduction may be limited by habitat conditions, accumulation of deleterious mutations over time, or inability to adapt to novel or changing conditions (Hellings and Gallagher 1992; Amsberry *et al.* 2000; Bart and Hartman 2000, 2003; Vasquez *et al.* 2005). We used nuclear genetic markers to determine whether *Phragmites* appears to be reproducing primarily by seed or rhizomes in Utah wetlands.

Assessment of gene flow among wetlands

In order to implement effective control strategies for introduced *Phragmites*, it is critical to understand the extent of gene flow among Utah wetlands. Gene flow and colonization patterns can be determined both by reproduction strategies (seed vs. rhizome, see above) and dispersal mechanism (wind, water, wildlife, and/or human-mediated dispersal). Genetic tools can be used to assess dispersal by comparing the genetic similarity of wetlands separated by different types of intervening habitats and geographic distances. If dispersal is extensive, allele frequencies at different genetic loci are expected to be quite similar among sites. If dispersal is restricted, allele frequencies at different genetic loci are expected to be distinct, with founder effects and genetic drift dictating local proportions of alleles. The geographic distance among genetically similar sites may provide insights about the mechanism(s) of dispersal. We used nuclear genetic markers to characterize allele frequency differences among introduced *Phragmites* populations in various Utah wetlands.

***Threats to native* Phragmites *populations – hybridization with and replacement by introduced* Phragmites**

In order to protect native *Phragmites* populations in Utah, we need to know if it is being replaced by or is hybridizing with introduced *Phragmites*. Historical records of native *Phragmites* populations in Utah are archived via herbarium specimens at universities such as Utah State University and Brigham Young University (Kulmatiski *et al. In press*). We can revisit these locations to determine if native *Phragmites* still exists or if it has been taken over by introduced *Phragmites*.

To detect hybridization between native and introduced *Phragmites*, we can assess the nuclear genetic signatures (banding patterns of, for example, AFLPs) of different *Phragmites* individuals. These signatures can also be compared to chloroplast sequences for the same individuals, since chloroplast sequences are very distinct between native and introduced individuals (Saltonstall 2002). We would expect native and introduced *Phragmites* individuals to exhibit unique banding patterns while hybrids would have intermediate banding patterns.

Methods

Field sampling

Introduced Phragmites. We collected *Phragmites* leaves from 10 sites in northern Utah/southern Idaho: two at Bear Lake, six at Great Salt Lake, two at Utah Lake (Figure 1a) that contained substantial stands of introduced *Phragmites*. Each site was separated by a distance of at least 10 km. At each site, we collected leaves from 5 sampling areas 100-500 m apart. At each sampling area within a site, we collected leaves from 5 different individuals separated by 10-30 m. We recorded GPS coordinates (Garmin eTrex Vista HCx, Garmin International, Olathe, KS) at each leaf collection point. In total, we collected 250 leaf samples.

Native Phragmites. We collected *Phragmites* leaves from 11 sites in northern Utah (Figure 1b) that were historically known to have native *Phragmites* (Kulmatiski *et al. In press*). All field methods were identical to those for introduced *Phragmites* except we used 6 sampling areas because we wanted to ensure that we had enough samples of native *Phragmites* leaves (in some areas there might also have been introduced *Phragmites*) and because we hypothesized that there might be a higher incidence of multiple samples from a clone if native *Phragmites* spreads more by rhizomes. Also, in a couple sites, the spatial spread of native *Phragmites* was too small to allow for 6 samplings areas 100-500m apart. In these situations, we simply maximized the distances among the 30 leaf samples taken at that site.

Genetic analysis

Leaves as young as possible were collected in order to improve DNA yields. A sample of at least 1 cm^2 was obtained from each individual plant and placed in a labeled paper envelope. Sample envelopes were placed in a container of silica gel desiccant beads to preserve DNA and prevent tissue decomposition. In the Utah State University Molecular Ecology laboratory, DNA was extracted from leaf tissue using a QIAGEN DNEasy 96 Plant Kit, and DNA quantity and size were assessed on 0.7% agarose gels stained with ethidium bromide and containing appropriate molecular weight and concentration standards.

Polymerase chain reaction (PCR) was used to amplify 10 nuclear microsatellite loci using protocols described by Saltonstall (2003). Only seven of these loci showed utility in Utah introduced *Phragmites*: One locus (PaGT8) was monomorphic for allele size 191 bp; one locus (PaGT11) was monomorphic for a particular genotype (157 and 161 bp), and one locus (PaGT21) was not scorable. The remaining 7 loci were amplified and scored for all samples. We included 35 replicated samples (replicate aliquots of DNA extractions) in our analyses in order to assess error rates in amplification, sample handling/labeling, analysis, and scoring. No scoring inconsistencies were detected among replicate samples.

We obtained complete 7-locus genotypes for 248 individual introduced *Phragmites* plants; two genotypes were missing data at a single locus. Allelic diversity overall was low, with only 2-4 alleles per loci observed. Only 6 microsatellite loci could be amplified reliably in the native individuals, and one of these had no variation across all individuals. In the remaining 5 loci, variation was also extremely low, with 1-3 alleles per locus in native populations. This low diversity limited the statistical power of our inferences so here we mostly rely on the results of the AFLP analyses. Low allelic diversity is expected in recently invading species, but is also a limitation of this published set of microsatellite loci (Saltonstall 2003).

Because of the low variation found in published microsatellite loci, we employed an additional molecular marker system, Amplified Fragment Length Polymorphism (AFLP) analysis. These analyses were conducted using a protocol originally by Vos *et al*. (1995) with modifications described in Mock *et al.* (2004). We used the following five selective primer combinations (*5' 6-FAM labelled): *Eco-AAC/Mse-AGC;*Eco-ACC/Mse-MACT; *Eco-ACG/Mse-ACA; *Eco-ACG/ Mse-ATC; *Eco-AGG/Mse-ACT. The amplicons were separated on a sequencing gel with a ROX 400 (Applied Biosystems) size standard using an ABI 3100 automated sequencer. Individual profiles were visualized and scored for each selective primer combination using Genographer 1.6 software (Benham 2001). Markers were scored if they were polymorphic (95% criterion) and could be scored unambiguously across the data set. Scoring was performed without reference to sample or population identity. A total of 107 and 105 polymorphic loci were scored across all native and introduced samples, respectively. Native and introduced samples were scored separately since band-sharing between these sample sets was low, and the requirement of unambiguous scoring in both sets for all loci would have reduced the number of useable loci within each set.

Data analysis

Genetic data for all plant samples was assembled and quality control replicates checked using GenAlEx software (Peakall and Smouse 2006), both for microsatellite analyses and AFLP analyses. GenAlEx software was also used to identify identical genotypes from different samples (clones) and to assess the probability of observing identical genotypes in sexually-derived individuals based on observed population allele frequencies (Waits *et al.* 2001). Deviations from Hardy-Weinberg and genotypic equilibria were assessed using GenePop software (Raymond and Rousset 1995a). Genetic distances among sites were characterized by constructing a matrix of Reynolds (1983) coancestries and Nei's (1972) distances, and these matrices were used to construct UPGMA dendrograms using TFPGA software (Miller 1997). Bootstrap replicates (1000x) were used to assess the relative strength of dendrogram nodes.

Exact tests (Raymond and Rousset 1995b) were used to determine whether samples from different sites could be genetically distinguished based on site-specific allele frequencies, using TFPGA software (Miller 1997). In order to determine the probability of individual observed genotypes having been derived from the site where they were sampled (as opposed to other sampled sites), we conducted an individual-based assignment test using GenAlEx software (Peakall and Smouse 2006) with the 'leave one out' procedure. We assessed the proportion of molecular variance attributable to site-specific differences by estimating F_{ST}, which ranges in value from 0 (implying no site-specific structure; all variance among individuals) to 1 (all variance due to site-specific differences; no variance among individuals within sites). Site structure was also characterized using an Analysis of Molecular Variance (AMOVA; Excoffier

et al. 1992). F_{ST} analyses were performed using TFPGA software (Miller 1997), and AMOVA analyses were performed using GenAlEx software (Peakall and Smouse 2006).

With AFLP data, a mismatch distribution was constructed to assess the presence of somatic variants vs. sexually generated genotypic variants. This distribution allowed us to pool AFLP genotypes that varied by only one to four mutations, and to distinguish them from genotypes that were sexually generated, which differed by 15 to 60 mutations.

Results and Interpretation

1- What is the relative importance of spread by seed for native vs. introduced* Phragmites*?
We found multiple lines of evidence indicating that introduced *Phragmites* is sexually reproducing and that there is substantial spread by seed within and among the sites we sampled compared with native *Phragmites*. First, we found more genetic diversity for introduced vs. native *Phragmites*, observing 76% unique multilocus genotypes for introduced *Phragmites* compared with 33% for native *Phragmites* (AFLP data). Second, introduced *Phragmites* genotypes at each site were found to be in Hardy Weinberg equilibrium (microsatellite data), suggesting that alleles are assorting randomly among individual genotypes through sexual recombination (i.e. seed production). Even when we considered all sites as one population, all but one loci were in Hardy Weinberg equilibrium. Thus, we were unable to reject the hypothesis of random mating within sites, and even among sites. These results suggest that there is substantial seed-based reproduction and gene flow within and among sites for introduced *Phragmites*. (We were not able to do comparable Hardy-Weinberg analyses for native *Phragmites* because the microsatellite markers were not variable enough to use them.) Third, when we evaluated overall diversity among introduced vs. native *Phragmites* (averaging across all populations), the percent polymorphic loci (90.1% vs. 65.1%) and gene diversity (0.29 vs. 0.20) were higher for introduced vs. native *Phragmites*, respectively (AFLP data). Fourth, the sizes of clones within populations were much larger for native *Phragmites* than introduced (AFLP data; see Question 4 below). Fifth, we found greater gene flow among introduced vs. native *Phragmites* populations (AFLP data; see Question 6 below). Thus, we conclude that introduced *Phragmites* is dispersing both within and among sites by seeds at greater rates than native *Phragmites*, and that this introduced *Phragmites* dispersal is occurring over large geographic distances (e.g. Bear Lake to Utah Lake). Given the range of geographic distances among sites, we could not determine whether seeds are spread primarily by wind, water, wildlife, humans, or some combination of these dispersal mechanisms.

2- Does* Phragmites *spread by rhizomes? We found evidence that both native and introduced *Phragmites* spread by rhizomes within sites. For native *Phragmites*, identical genotypes between samples were found in all sites and for introduced *Phragmites*, identical genotypes were found between samples within all sites except the Great Salt Lake State Marina (Tables 1a and 1b; Figures 2a and 2b; AFLP data). We found no instances of spread by rhizomes among sites for either introduced or native *Phragmites* (AFLP data). In other words, there were no identical genotypes found at multiple sites.

3- How many clones exist within a site? For introduced *Phragmites*, the number of clones within a site ranged from 9 at Bear Lake West to 23 at the Great Salt Lake State Marina (Table 1a; AFLP data). In other words, all samples taken from the Great Salt Lake State Marina were

genetically different from each other and represented different clones, while all other sites contained a mixture of genetically unique samples and genetically identical samples. For native *Phragmites*, we found many fewer clones within a site in general; all samples at Bakers Hot Springs represented one clone, all samples at Mystic Hot Springs represented just two clones, and all samples in Nine Mile Canyon represented just three clones (Table 1b; AFLP data). There were a few exceptions to this rule, however, particularly for the San Rafael River site (native) that had 21 clones. We do not know whether plants with genetically identical samples are (or once were) connected via rhizomes or whether these are cases of short-distance rhizome dispersal within a site, but we suspect both situations given the spatial occurrence of clones within sites. There is no obvious large-scale spatial pattern to the observed number of clones per site for native or introduced *Phragmites*. For instance, the two introduced *Phragmites* sites at Bear Lake had one of the lowest and one of the highest numbers of clones within a site.

4- What is the spatial distribution of clones within a site? Figures 2a and 2b illustrate the spatial distribution of clones among the samples taken at each site (AFLP data). In most cases for introduced *Phragmites,* genetically identical samples were found within a sampling area, i.e., those samples were 10-30 m apart. However, at two of the ten sites (Utah Lake West, Utah Lake East) identical genotypes were found across the different sampling areas within a site. In other words, those genetically identical samples were found $\geq$100 m apart. Often we were not able to sample native *Phragmites* in discrete sampling areas because of the natural distribution of individuals in the field. However, we found multiple instances of genetically identical samples at >100 m apart (e.g., Nine Mile Canyon and Fish Springs National Wildlife Refuge, Figure 2a). Also, at two other sites (Clear Creek and Springville), genetically identical samples were not only found at large distances from each other but also across roads.

5- How genetically similar are different sites? There were two main groupings of introduced *Phragmites* across the sites sampled in Northern Utah wetlands (Figure 3a; AFLP data). The Reynold's coancestry matrix, Nei's genetic distance matrix, and pairwise population exact tests suggested similar groupings of sites. The two Utah Lake sites and the Inland Sea Shorebird Reserve were genetically similar and the remaining seven sites clustered because they were genetically similar. Genetic distinction between these two clusters indicate some gene flow restriction which fails to homogenize allele frequencies. There were three main groupings of native *Phragmites* (Figure 3b). One group was comprised of plants from Springville (east side of Utah Lake), Utah Lake West, and Fish Springs National Wildlife Refuge. Four other sites clustered into a second grouping: Green River, Ouray National Wildlife Refuge, Willow Creek, and Nine Mile Canyon. Finally, plants from Clear Creek, the San Rafael River, Mystic (Monroe) Hot Springs, and Baker Hot Springs formed a third cluster because of their genetic similarity.

6- How much of the genetic variability is found within a site versus among sites for native vs. introduced* Phragmites*? The AMOVA results (AFLP data) indicate that 91% of the molecular variation in the dataset was found within sites and 9% was found among sites for introduced *Phragmites* (Figure 4). For native *Phragmites*, 35% was found among sites and 65% was found within sites (Figure 4). The F_{ST} values (Weir and Cockerham's theta, θ_{ST}) support these results. For introduced *Phragmites*, $\theta_{ST} = 0.11 \pm 0.03$ (standard deviation) and for native *Phragmites*, $\theta_{ST} = 0.38 \pm 0.02$. These results indicate that there is low, albeit significant, levels of site differentiation for introduced *Phragmites* and that there is substantial gene flow (i.e. low genetic

differentiation) among sites. For native *Phragmites*, there is a much greater among site differentiation indicating that gene flow among sites is more limited compared with introduced *Phragmites*.

***7-Is hybridization occurring between native and introduced* Phragmites?**
We found no evidence that native and introduced *Phragmites* are hybridizing. The banding patterns in the AFLPs were distinct for native vs. introduced *Phragmites*.

***8- Is introduced* Phragmites *replacing native* Phragmites?**
In all instances, we were able to relocate the historic populations of native *Phragmites* that we were searching for. Of the 11 native *Phragmites* sites, however, two of them had substantial introduced *Phragmites* present as well. Both sites were located along Utah Lake, one on the east side and one on the west. We were not able to determine whether native *Phragmites* has actually been reduced or displaced in terms of coverage by introduced *Phragmites* at these sites; there is certainly a risk of that occurring in the future. We could only determine if native *Phragmites* is still present, which it was.

9- How similar are the genetic patterns of introduced* Phragmites *in Northern Utah to* Phragmites *invading other regions of the US? We compared the results of the present study to work done by Karin Kettenring with colleagues studying *Phragmites* invasion in the Chesapeake Bay (McCormick *et al. In press*). The level of diversity in Northern Utah is approximately half that of *Phragmites* invading the Chesapeake Bay (based on number of alleles per locus observed). This finding is not surprising because *Phragmites* invasion in Utah is likely more recent and thus we would expect lower levels of genetic diversity. Unfortunately, as additional invading genotypes arrive in Utah, genetic diversity in introduced *Phragmites* is likely to increase, potentially also increasing its ability to adapt and persist.

Summary and Management Implications

We demonstrate that introduced *Phragmites* is spreading both by seeds and by rhizomes within and among sites at Bear Lake, Great Salt Lake, and Utah Lake but that there is a greater amount of spread by seed compared with native *Phragmites*. Multiple lines of evidence suggest that there is substantial gene flow among the 10 introduced *Phragmites* sites we sampled across Northern Utah, especially when compared with native *Phragmites*. Taken together, our findings suggest that efforts to control the spread of introduced *Phragmites* should consider means to minimize *Phragmites* sexual reproduction and spread by seed, as well as spread via rhizome dispersal. Currently, most *Phragmites* control efforts consist of a fall herbicide (glyphosate) spray and a subsequent burn. Additional efforts like mowing in early summer to prevent seed production may improve control efforts (Kettenring *et al.* 2010). Otherwise, *Phragmites* can continue to produce seeds and can simply recolonize by seed after herbicide has killed the existing vegetation. At the same time, any control efforts that may break up and disperse rhizomes (like tilling or disking) may actually enhance *Phragmites* spread. We suggest that a comprehensive approach to *Phragmites* control should take into account that this plant is spreading by rhizomes, and contrary to popular opinion, by seeds. Furthermore, efforts to limit any displacement of native *Phragmites* by introduced *Phragmites* will be crucial, especially at sites along Utah Lake.

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Tables

Table 1a. Variation in the number of introduced *Phragmites* clones in each of the 10 study sites (AFLP data).

Site	# samples	# of clones	# clones / sample
Bear Lake West	24	9	0.38
Bear Lake East	25	23	0.92
Bear River North	25	20	0.80
Bear River South	25	15	0.60
Farmington Bay Waterfowl Management Area	25	19	0.76
Ogden Bay Waterfowl Management Area	25	19	0.76
Inland Sea Shorebird Reserve	25	22	0.88
Great Salt Lake State Marina	23	23	1.00
Utah Lake West	25	14	0.56
Utah Lake East	25	21	0.84

Table 1b. Variation in the number of native *Phragmites* clones in each of the 11 study sites (AFLP data).

Site	# samples	# of clones	# clones / sample
Baker Hot Springs	30	1	0.03
Clear Creek	30	5	0.17
Fish Springs National Wildlife Refuge	29	16	0.55
Green River	28	5	0.18
Mystic Hot Springs	30	3	0.10
Nine Mile Canyon	30	3	0.10
Ouray National Wildlife Refuge	33	15	0.45
Springville, Utah	30	7	0.23
San Rafael River	30	21	0.70
Utah Lake	29	13	0.45
Willow Creek	29	11	0.38

Figures

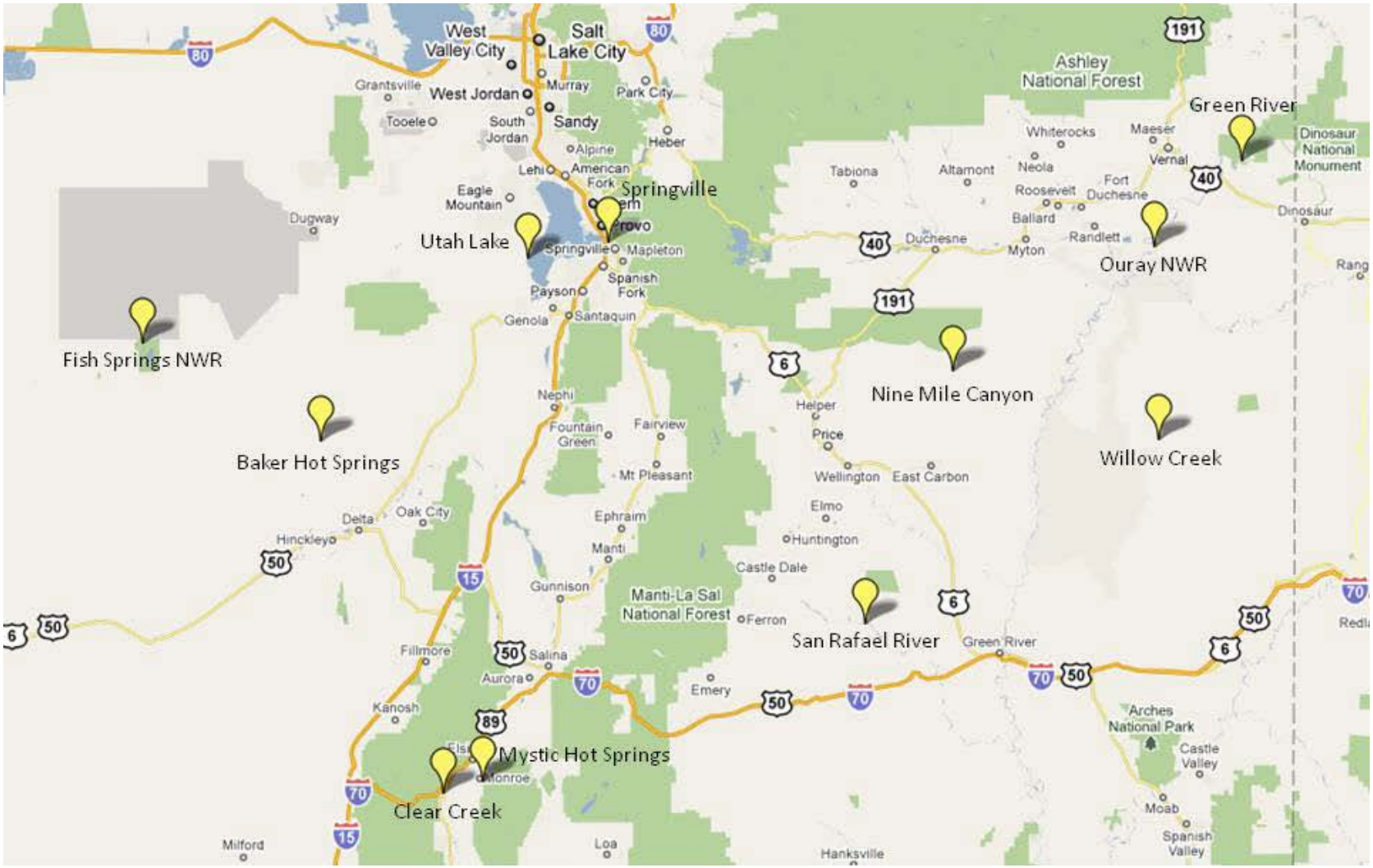


Figure 1a. The locations of the 11 native (in yellow) *Phragmites* sites.

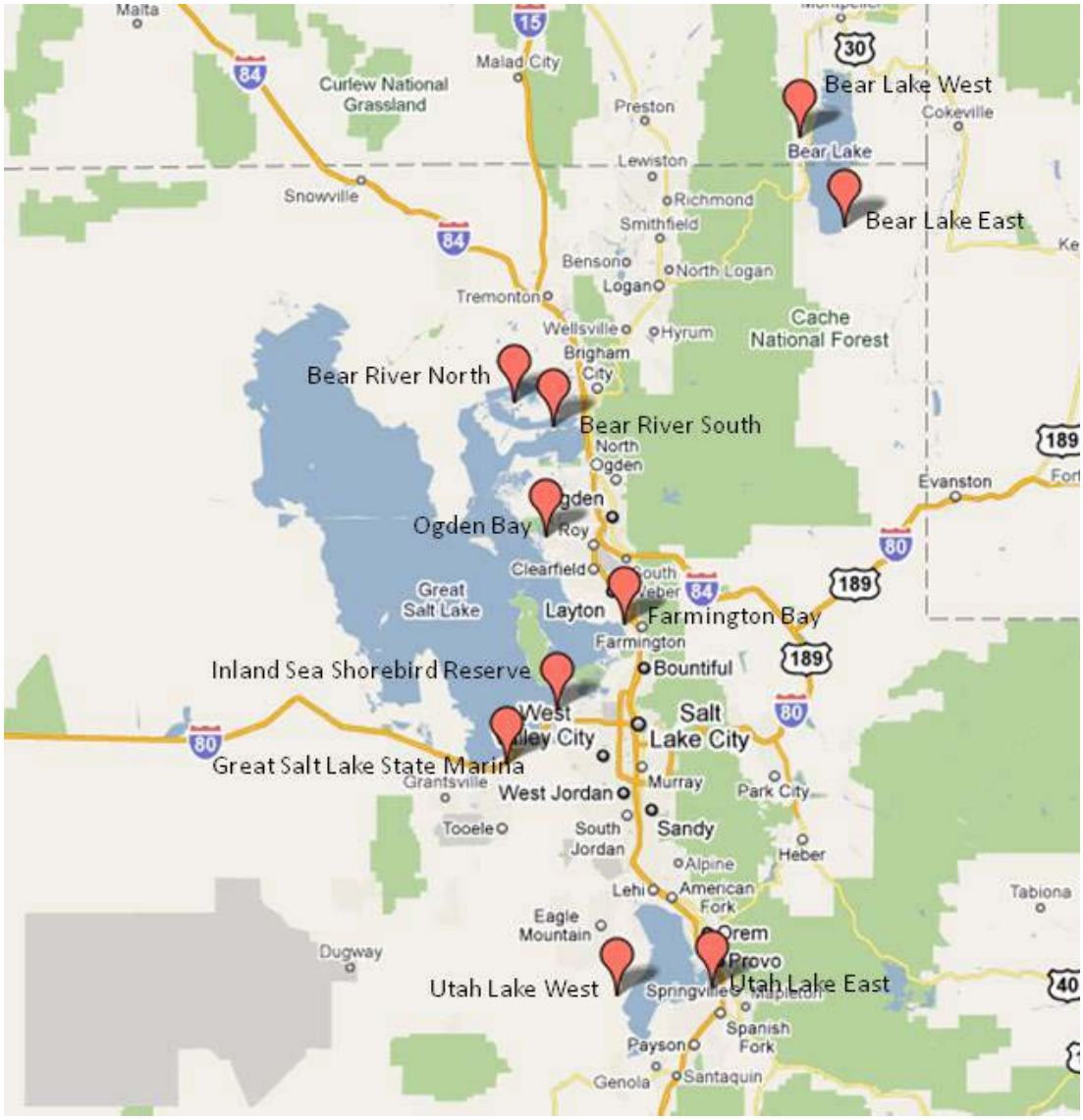
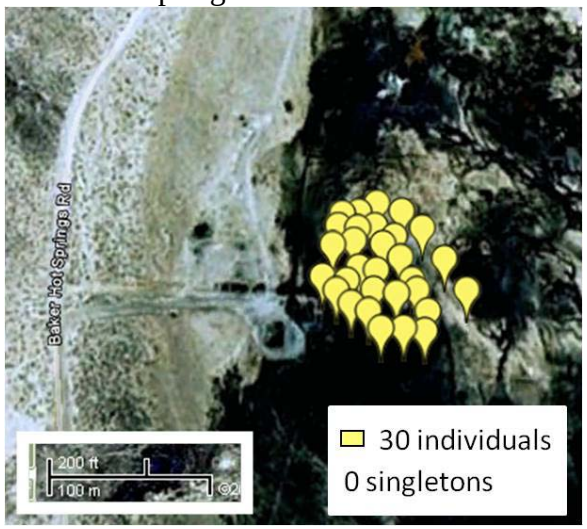
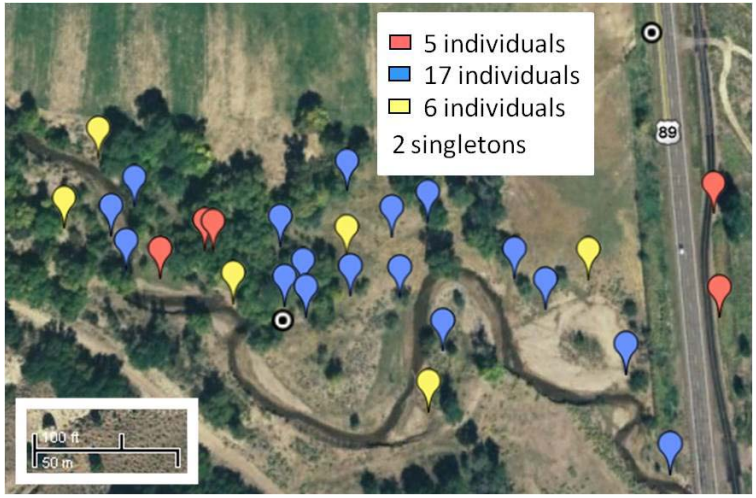


Figure 1b. The locations of the 10 introduced (in red) *Phragmites* sites.

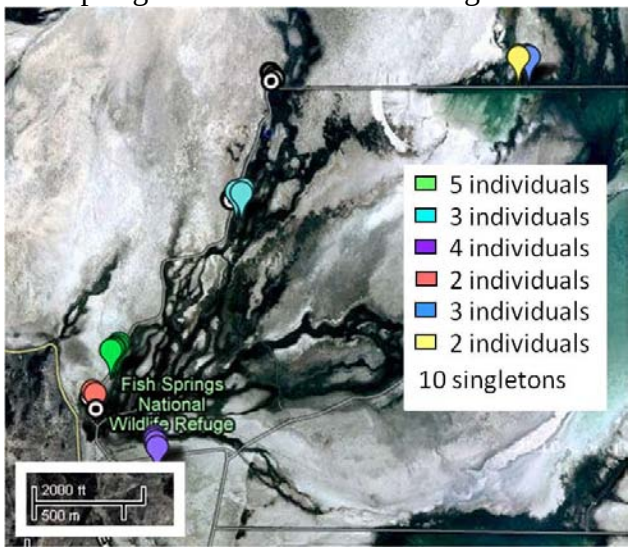
Baker Hot Springs



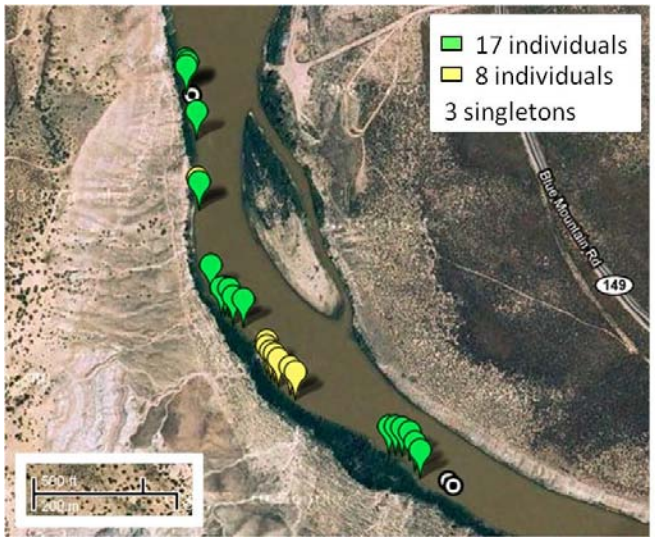
Clear Creek



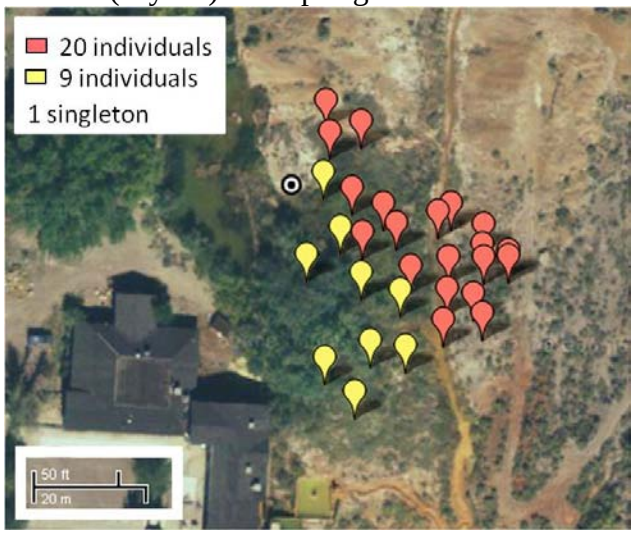
Fish Springs National Wildlife Refuge



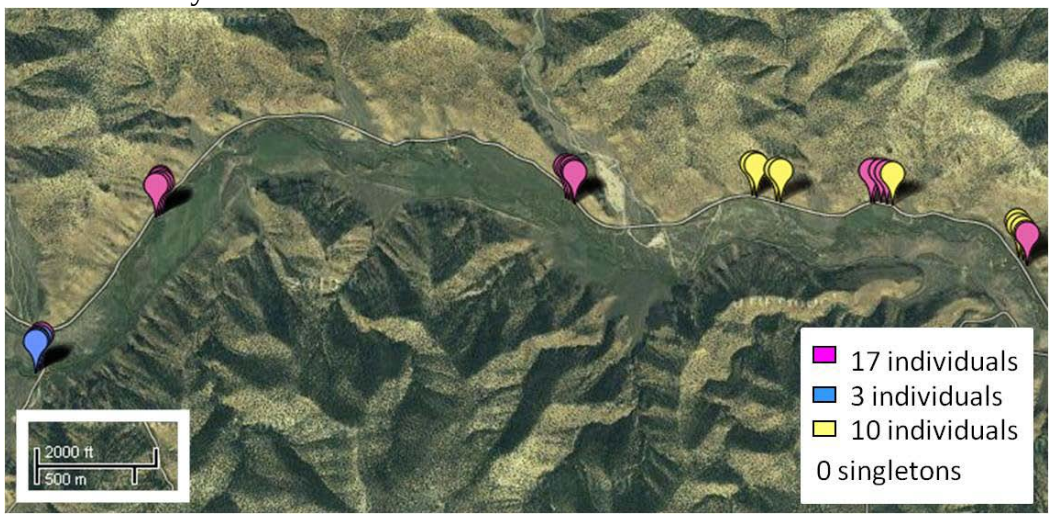
Green River



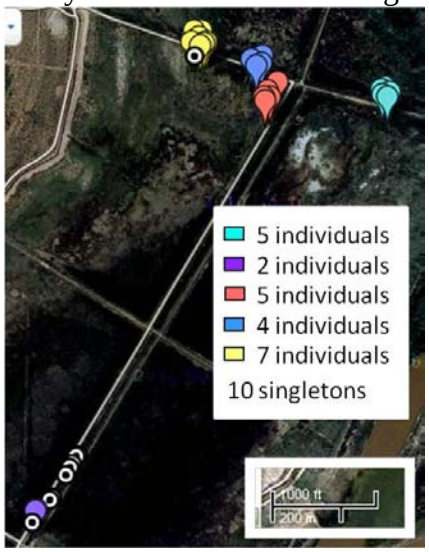
Monroe (Mystic) Hot Springs



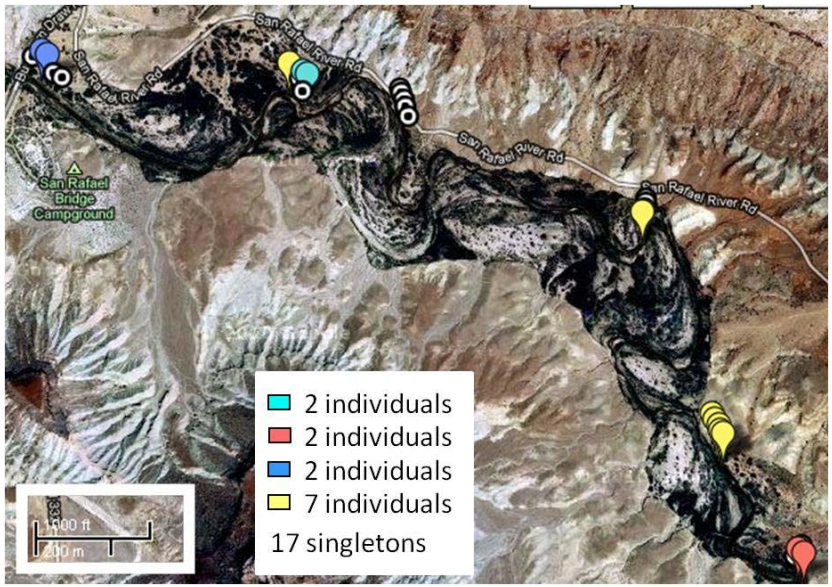
Nine Mile Canyon



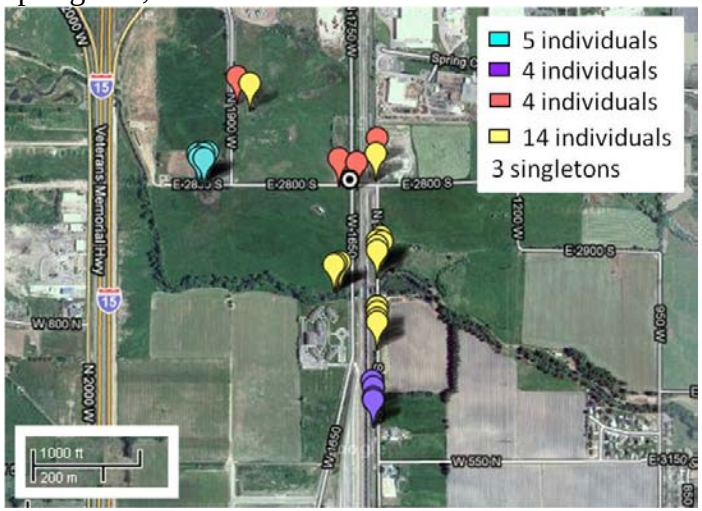
Ouray National Wildlife Refuge



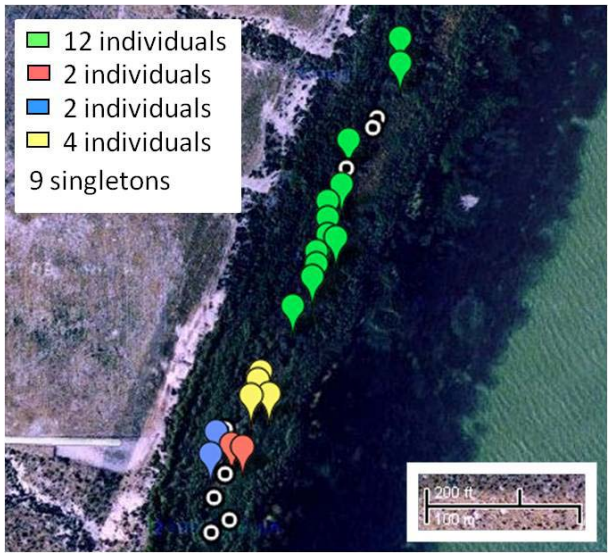
San Rafael River



Springville, Utah



Utah Lake Native

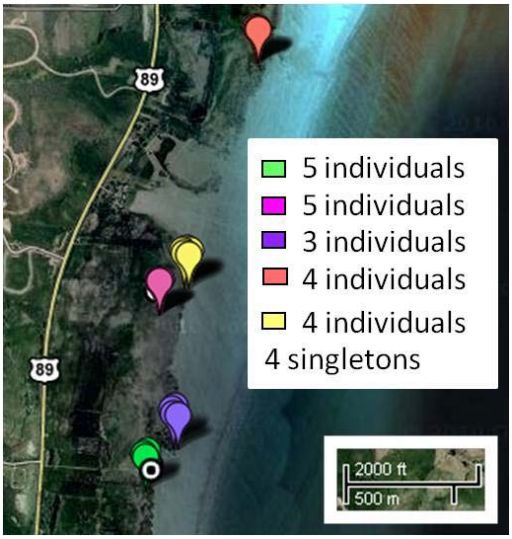


Willow Creek

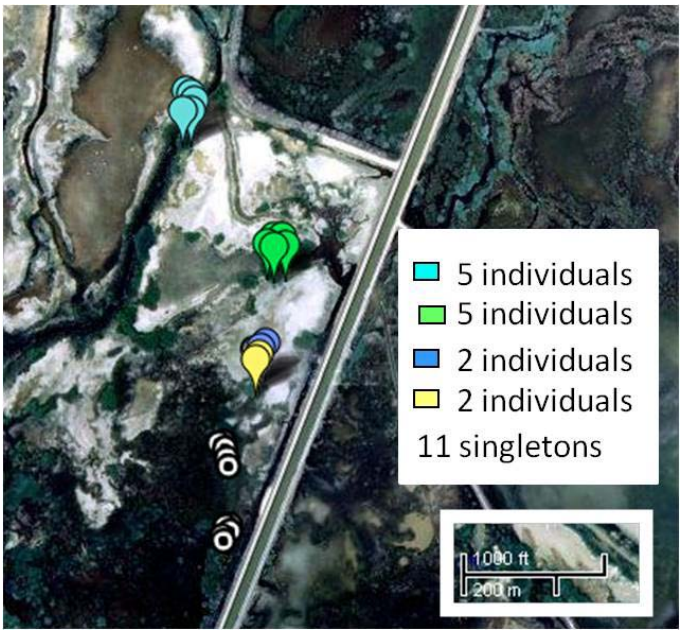
Figure 2a. The distribution of clones and individual genotypes in each of the 11 native *Phragmites* sites (AFLP data). All place markers with the same color at a site represent individuals from the same clone. Singletons are genotypes that were observed only once at a site and are denoted in all maps with a black and white “bulls-eye”.

Bear Lake East

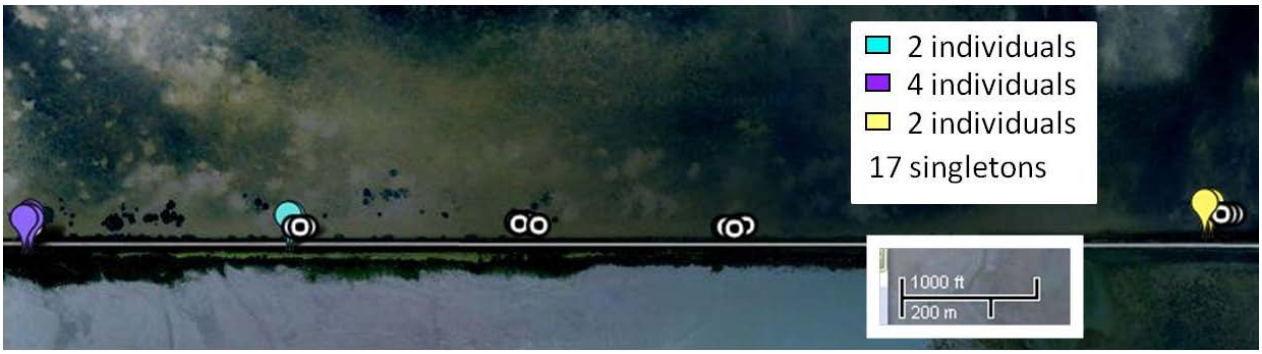
Bear Lake West



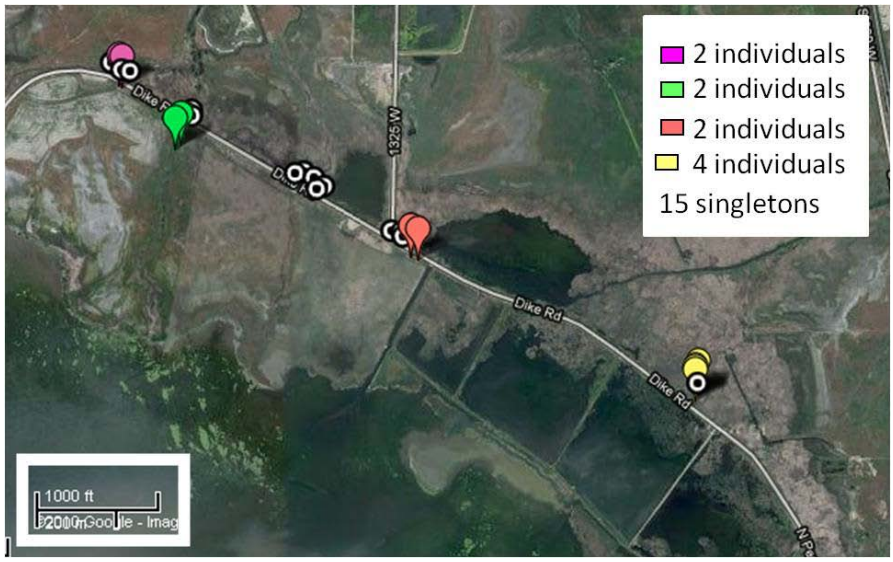
Bear River North



Bear River South

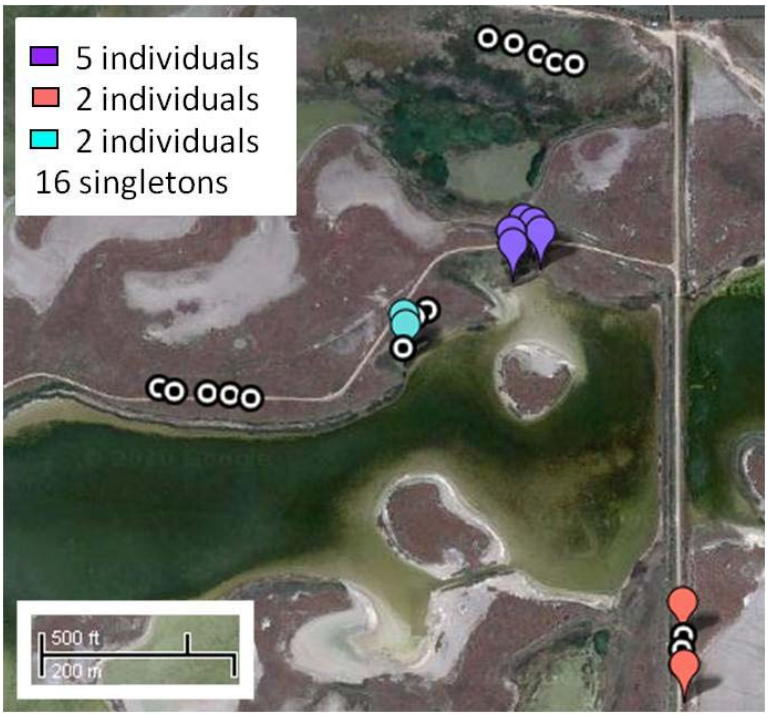


Farmington Bay Waterfowl Management Area

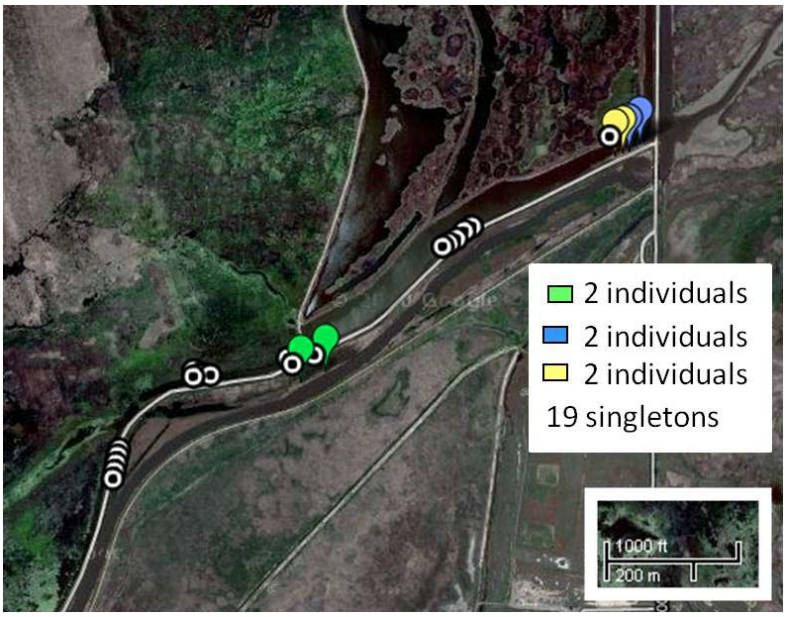


Great Salt Lake State Marina

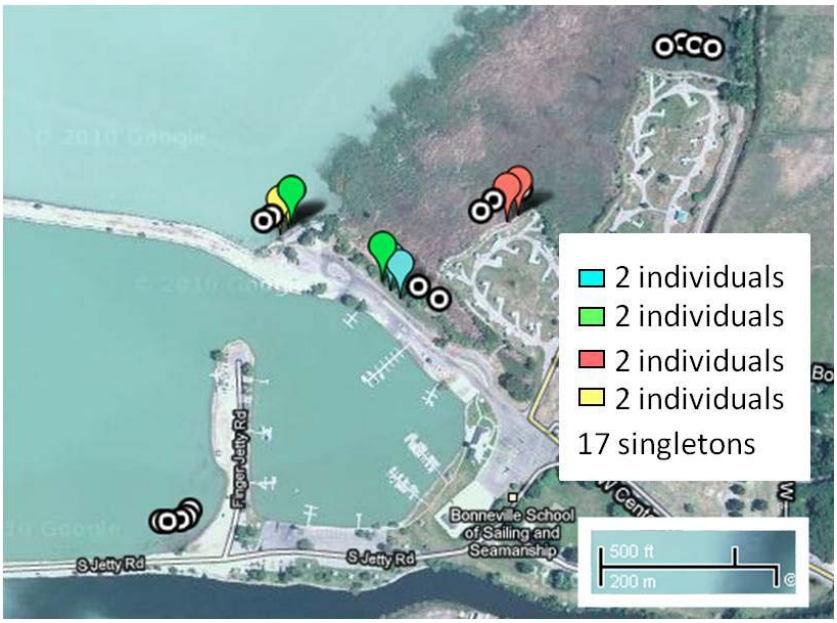
Inland Sea Shorebird Reserve



Ogden Bay Waterfowl Management Area



Utah Lake East



Utah Lake West

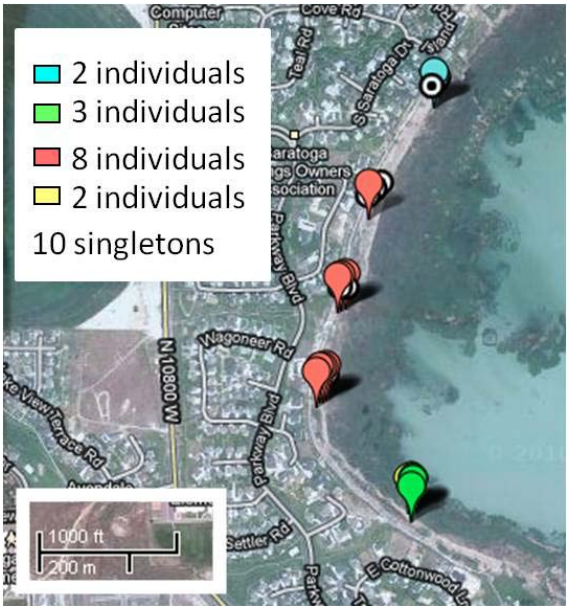
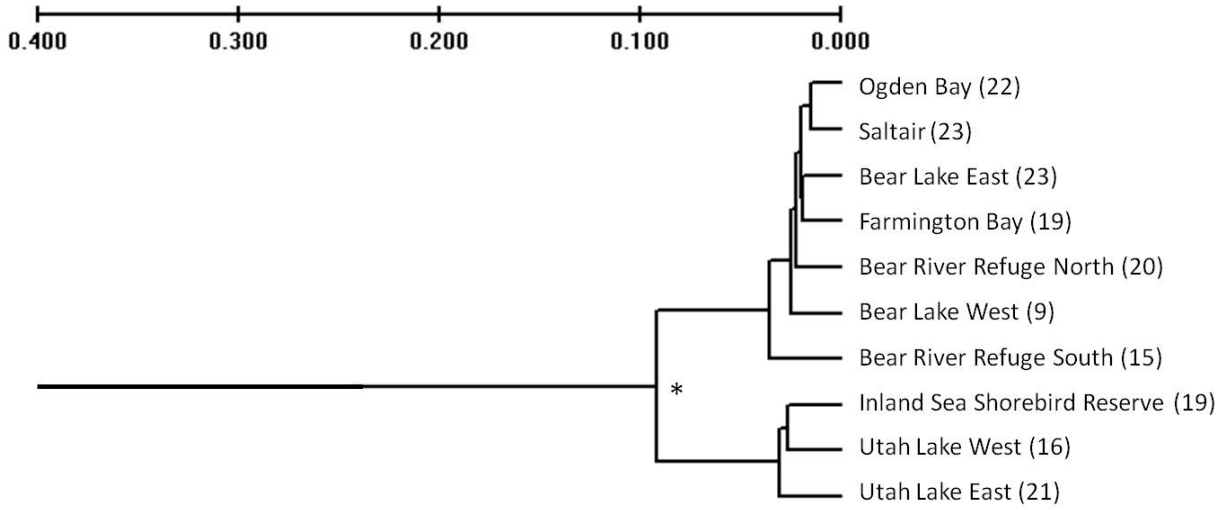


Figure 2b. The distribution of clones and individual genotypes in each of the 10 introduced *Phragmites* sites (AFLP data). All place markers with the same color at a site represent individuals from the same clone. Singletons are genotypes that were observed only once at a site and are denoted in all maps with a black and white “bulls-eye”.

a.



b.

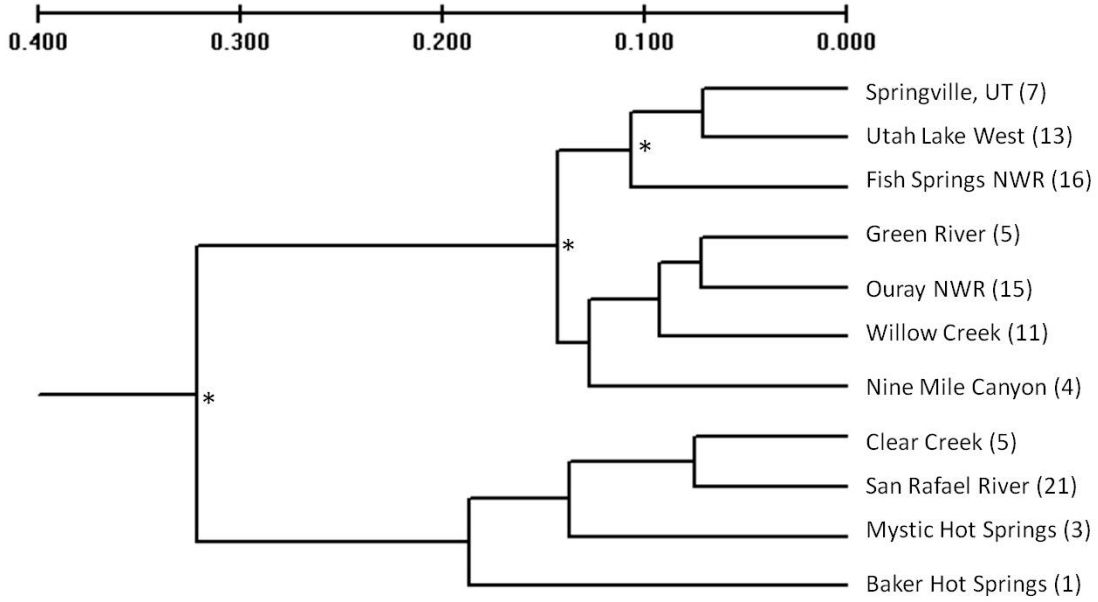


Figure 3. Nei's genetic distances among sampling sites for (a) introduced *Phragmites* and (b) native *Phragmites* (AFLP data). Asterisks denote branches that are significantly different at $\alpha = 0.05$ based on Exact Tests. The numbers in parentheses represent the number of genetically unique samples from each site that were used to determine the genetic distances and run the Exact Tests.

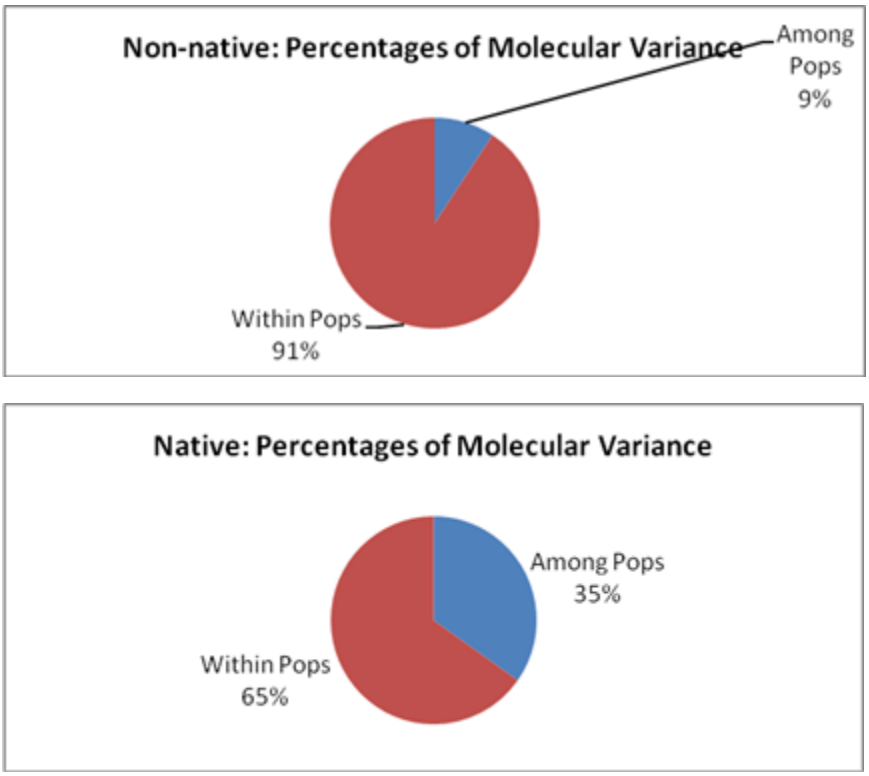


Figure 4. Results from the Analysis of Molecular Variance (AMOVA; AFLP data).