

Epigenetic variation within *Phragmites australis* among lineages, genotypes, and ramets

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to microhabitat conditions where multiple genotypes exist across a heterogeneous environment.

Methylation-sensitive amplified fragment length polymorphisms (MS-AFLPs)

We screened 96 individuals for epigenetic variation

of the total variance could be explained by the 2010 Herrera and Bazaga2011). However, the segregation of individuals according to subspecies limited variation due to genotype we observed (Table 1). In addition to demonstrating distinct epigenetic signatures, our results support the theory that aligned with environmental factors among ramets. conspecifics exhibit consistent variation from large-scale morphological characteristics to smaller-scale physiological and epigenetic responses.

Plasticity has been proposed as one characteristic highest source of variance among samples. Genotype that promotes invasion (Pal1998; Richards et al.2006; Davidson et al.2011; Richards et al.2012). Being more plastic allows a species to act as a generalist, Webhannet site and 7 % of epigenetic variance at the Libby site (hierarchical AMOVA, Table 1). By comparing a broad niche in its environment. The generalist approach permits the establishment of statistically significant variation among genotypes in invasive populations in heterogeneous, unstable or rapidly changing environments (Pal1998). This appears to be consistent with P. australis populations. The native stands are often restricted to growing in low-salinity tidal wetlands, whereas clones of the introduced subspecies can span diverse microhabitats from mesohaline marshes to tidal wetlands to freshwater river systems (Chambers et al.1999). The broad introduced distribution could be facilitated by high levels of variation in epigenotype. Our results show that the invasive introduced subspecies is more epigenetically plastic than the native, however, at this stage we do not know if this lack of epigenetic plasticity within the native is limiting its expansion.

In both subspecies we observed a higher degree of epigenetic variation within rather than between-genotypes. While environmental variation was not directly measured here, there is considerable evidence in the literature that epigenotype is largely influenced by genotype and environmental factors (Bossdorf et al. 2014). As a clone adjusts to optimize its resource extraction and growth, it may prove

Table 1 AMOVA derived from Webhannet and Libby sites, separately, showing percentage variation explained by subspecies, genotypes, and ramets

Source	df	Sum of squares	Mean of squares	Estimated Variance	%	p value
Webhannet Marsh (n = 46 invasive, n = 47 native)						
Among subspecies	1	284.932	284.932	5.174	25	0.001
Among genotypes	1	28.908	28.908	0.794	4	0.022
Within genotypes	90	1344.741	14.942	14.942	71	0.001
Total	92	1658.581		20.909	100	
Libby Marsh (n = 15 invasive, n = 15 native)						
Among subspecies	1	86.800	86.800	4.805	37	0.001
Among genotypes	4	41.030	10.258	0.859	7	0.066
Within genotypes	24	178.837	7.452	7.452	57	0.001
Total	29	306.667		13.116	100	

advantageous to differentiate ramets within the genet. Such local specialization would require a mechanism more nimble (fast, reversible, and sensitive to environmental variation) than the presence or absence of a gene, particularly within genetically uniform clones. Variability in epigenetic markers is a means of acclimation, potentially more rapid and responsive than adaptation, and thus practical over short to moderate amounts of time and space (Douhovnikoff and Dodd2014).

Natural selection acts to increase or decrease plasticity depending on environmental conditions, the rate at which conditions change, and the character of the species (Alpert and Simms2002, Davidson et al. 2011; Herman et al2013). The limited distribution of native *P. australis* large clone sizes, and relatively lower plasticity may indicate a life history strategy more dependent on stability, where it could be more advantageous to specialize in a narrow niche (Alpert and Simms2002, Douhovnikoff and Dodd2014). However, this does not minimize the importance of

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