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ORIGINAL ARTICLE

Latitudinal variation in cold hardiness in introduced *Tamarix* and native *Populus*

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Abstract

To investigate the evolution of clinal variation in an invasive plant, we compared cold hardiness in the introduced saltcedar (Tamarix ramosissima, Tamarix chinensis, and hybrids) and the native plains cottonwood (Populus deltoides subsp. monilifera). In a shadehouse in Colorado (41°N), we grew plants collected along a latitudinal gradient in the central United States (29-48°N). On 17 occasions between September 2005 and June 2006, we determined killing temperatures using freeze-induced electrolyte leakage and direct observation. In midwinter, cottonwood survived cooling to -70°C, while saltcedar was killed at -33 to -47°C. Frost sensitivity, therefore, may limit northward expansion of saltcedar in North America. Both species demonstrated inherited latitudinal variation in cold hardiness. For example, from September through January killing temperatures for saltcedar from 29.18°N were 5-21°C higher than those for saltcedar from 47.60°N, and on September 26 and October 11, killing temperatures for cottonwood from 33.06°N were >43°C higher than those for cottonwood from 47.60°N. Analysis of nine microsatellite loci showed that southern saltcedars are more closely related to T. chinensis while northern plants are more closely related to T. ramosissima. Hybridization may have introduced the genetic variability necessary for rapid evolution of the cline in saltcedar cold hardiness.

Introduction

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Native woody species often demonstrate inherited latitudinal variation in the timing of growth cessation and cold hardiness in response to the latitudinal gradient in temperature (Pauley and Perry 1954; Howe et al. 1995). Can an introduced species develop such a pattern in a century or two (Weber and Schmid 1998)? Development of clinal variation could be accelerated by multiple introductions of populations from different latitudes (Novak and Mack 2001), by hybridization between closely related species from different climates (Hurka et al. 2003), or by epigenetic inheritance of cold hardiness (Saxe et al. 2001). This question can be addressed by studies comparing clinal variation in native and introduced species.

The diploid genus *Tamarix* was introduced to North America in the mid-1800s to control erosion and to serve

as a drought-tolerant ornamental flowering shrub or tree (Robinson 1965). Although there are now several Tamarix species in the United States (USA), Tamarix chinensis Lour. and Tamarix ramosissima Ledeb. are by far the most abundant (Gaskin and Schaal 2003). Tamarix chinensis is native to China, Korea, and Japan at latitude 23-42°N and longitude 79-110°E, whereas T. ramosissima occurs more widely across temperate Asia at latitude 30-53°N and longitude 42-127°E (Baum 1978). Although these two species are morphologically distinct in Asia (Baum 1978), North American specimens cannot always be readily distinguished (Crins 1989). Hereafter, we refer to the complex of T. ramosissima, T. chinensis, and their hybrids as saltcedar. In a study of a single nuclear locus in saltcedar, Gaskin and Schaal (2002) found that the most common genotype in North America is a heterozygote containing one allele that in Asia is found only in

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