

Genetic and Environmental Influences on Cold Hardiness of Native and Introduced Riparian Trees

Jonathan M Friedman, James E Roelle, and Brian S Cade

Jonathan M Friedman is Research Hydrologist, US Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, CO 80526; E-mail: friedmanj@usgs.gov. **James E Roelle** is Biologist, US Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, CO 80526; E-mail: roelleb@usgs.gov. **Brian S Cade** is Research Statistician, US Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, CO 80526; E-mail: cadeb@usgs.gov

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Abstract: To explore latitudinal genetic variation in cold hardiness and leaf phenology, we planted a common garden of paired collections of native and introduced riparian trees sampled along a latitudinal gradient. The garden in Fort Collins, Colorado (latitude 40.6°N), included 681 native plains cottonwood (*Populus deltoides* subsp. *monilifera*) and introduced saltcedar (*Tamarix ramosissima*, *T. chinensis*, and hybrids) collected from 15 sites from 29.2 to 47.6°N in the central United States. In the common garden, both species showed latitudinal variation in fall, but not spring, leaf phenology. This suggests that latitudinal gradient field observations in fall phenology are a result, at least in part, of the inherited variation in the critical photoperiod. Conversely, the latitudinal gradient field observations in spring phenology are largely a plastic response to the temperature gradient. Populations from higher latitudes exhibited earlier bud set and leaf senescence. Cold hardiness varied latitudinally in both fall and spring for both species. Although cottonwood was harder than saltcedar in midwinter, the reverse was true in late fall and early spring. The latitudinal variation in fall phenology and cold hardiness of saltcedar appears to have developed as a result of multiple introductions of genetically distinct populations, hybridization, and natural selection in the 150 years since introduction.

Keywords: Cold hardiness, latitude, phenology, *Populus deltoides*, rapid evolution, *Tamarix*

Introduction

Because of the latitudinal gradient in temperature, wide-ranging species often display latitudinal gradients in phenology. Increasing latitude is typically associated with later leaf flush and flowering and earlier growth cessation, leaf senescence, and onset of cold hardiness (Sakai 1970, Ying and Bagley 1976). Latitudinal gradients in phenology reflect both genetic variation and a plastic response to the climatic gradient, and common-garden studies can be used to determine the relative importance of these factors (Colautti and others 2009). If phenological variation persists when plants from different latitudes are grown together, then the variation observed in the wild has a genetic component.

We examined phenology and cold hardiness in a common garden consisting of paired collections of a native and an introduced species. The selected species were cottonwood and saltcedar, riparian pioneer trees that compete for dominance along rivers throughout most of the western United States (Friedman and others 2005). Plains cottonwood (*Populus deltoides* Bartram ex Marsh. ssp. *monilifera* (Aiton) Eckenwalder) is the dominant riparian tree of the western Great Plains, ranging from northern Texas to southern Manitoba, Saskatchewan, and Alberta at latitude 30–55°N and longitude 96–114°W (USDA 2009). Riparian shrubs of the genus *Tamarix* were introduced to North America in the mid-1800s as ornamental plants and for erosion control. Although there are now several *Tamarix* species in the United States, *T. chinensis* Lour. and *T. ramosissima* Ledeb. are by far the most abundant (Gaskin and Kazmer 2009). Although these two species are morphologically and genetically distinct in Asia, the North American population is dominated by their hybrids (Friedman and others 2008, Gaskin and Kazmer 2009). We refer to the complex of *T. ramosissima*, *T. chinensis*, and their hybrids as saltcedar. Saltcedar is now the second most abundant riparian woody plant in the interior western United States (Friedman and others 2005).

A comparison of latitudinal gradients in cold hardiness and phenology in cottonwood and saltcedar is valuable for two reasons. First, it makes it possible to explore whether differences in cold hardiness could explain the apparent inferior competitive ability of saltcedar in the north. This information would help to assess the potential for spread of this major invasive species both in the present climate and in response to climate warming. Second, comparing latitudinal variation in the native and introduced species explores whether patterns of clinal variation typical of native species can rapidly evolve in introduced species.

Materials and Methods

In February and March of 2005, we collected plains cottonwood and saltcedar as cuttings from 15 sites distributed along a latitudinal gradient from 29.2 to 47.6°N in the central U.S. (Friedman and others 2008, 2011). On 16 August 2005, we planted rooted cuttings in a common garden at the Colorado State Nursery in Fort Collins at latitude 40.58°N and longitude 105.14°W. The garden contained 313 cottonwoods and 368 saltcedars planted in a clay loam soil in a random design.

In 2006, 2007, and 2008, a single observer made weekly phenological observations of plants in the common garden. We observed the dates of leaf flush and leaf senescence of both species and the date of terminal bud formation in cottonwood. We measured variation in cold hardiness of plant stems through time, within populations, between latitudes, and between species. To measure cold hardiness we cut a 40-cm twig into seven 5-cm pieces, placed the pieces in wire racks, and exposed them to seven different temperatures using a programmable temperature chamber. Post freezing, the stems were placed on racks in water at room temperature, incubated for two weeks, and then scored as live or dead (Calkins and Swanson 1990). We defined the killing temperature (LT50) as the temperature at which the probability of dying exceeded 0.50 and used logistic regression in SAS[®] (SAS Institute, Inc., Cary, NC) to estimate probability of dying as a function of temperature, latitude of origin, and species. A more detailed presentation of methods and results can be found in Friedman and others (2011).

Results

The timing of cottonwood terminal bud formation was strongly negatively correlated with latitude. Northern cottonwoods formed their terminal buds and ceased extension growth before southern cottonwoods (Figure 1). In the years 2006, 2007, and 2008, cottonwoods from latitude 47.6 formed buds 20 days, 37 days, and 23 days before cottonwoods from latitude 34.9, and the correlations between bud formation date and latitude were -0.66, -0.84 and -0.73.

The timing of leaf senescence for both species was also negatively correlated with latitude (Figure 1). Consistent with the latitudinal effect on bud formation, leaves of northern individuals of both species became senescent before those of southern individuals (Figure 1). The time difference between leaf senescence at latitudes 34.9 and 47.6°N was larger in cottonwood (21 days) than in saltcedar (10 days) and the correlation between latitude and leaf senescence date was stronger in cottonwood (-0.58) than in saltcedar (-0.37) (Figure 2). The timing of spring leaf flush was not correlated with latitude in cottonwood and weakly and inconsistently correlated with latitude in saltcedar. Leaf flush occurred earlier in saltcedar than in cottonwood by 22 days in 2007, and 21 days in 2008 (Figure 1).

Stems of both cottonwood and saltcedar survived colder temperatures in winter than in summer, but this seasonal cycle was stronger in cottonwood than in saltcedar (Figures 1 and 2); as a result cottonwood was harder in midwinter, but saltcedar was harder in the late spring and early fall. In autumn, killing temperatures

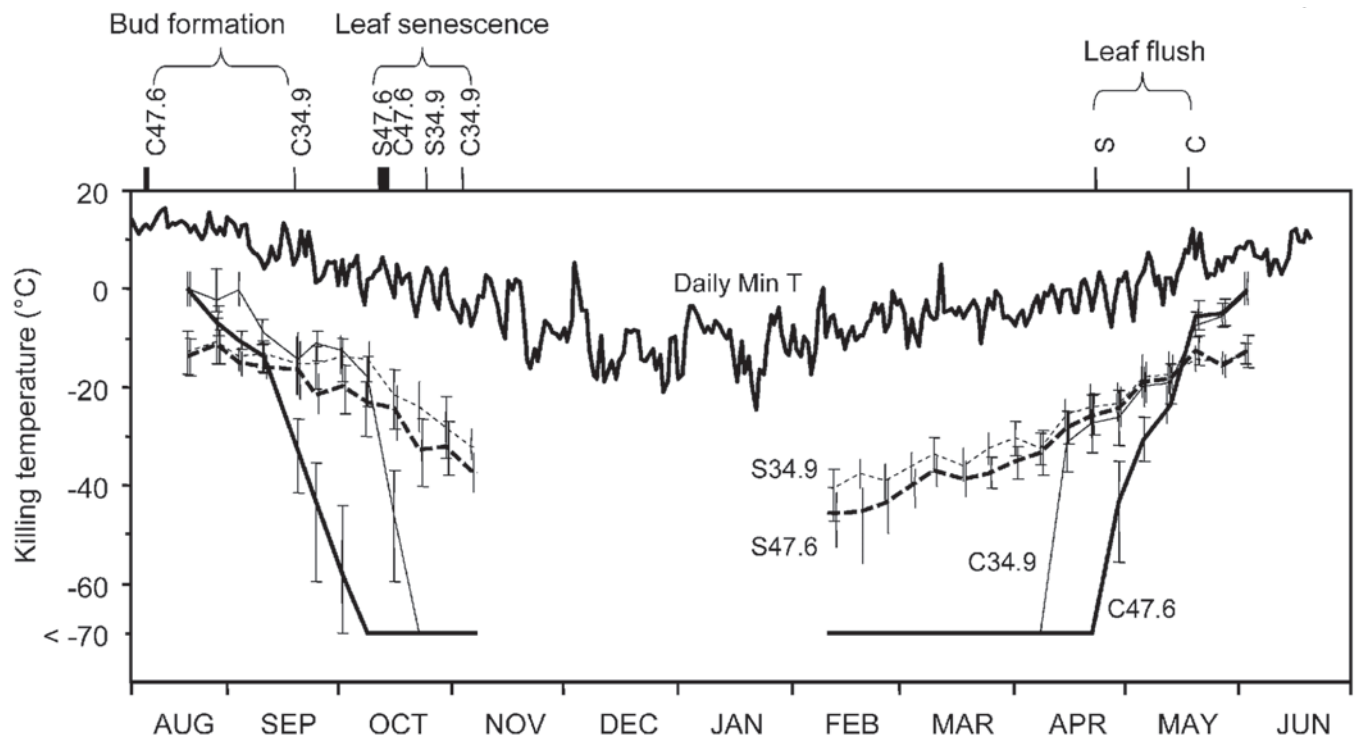


Figure 1. Temporal variation in killing temperature for twigs of northern and southern plains cottonwood (C) and saltcedar (S) grown in Fort Collins, Colorado (latitude 40.6°N) during fall 2007 and spring 2008. Northern individuals are from Fort Peck Reservoir, Montana, latitude 47.6°N and southern individuals are from Buffalo Lake National Wildlife Refuge, Texas, latitude 34.9°N. Mean values by species and latitude for timing of leaf flush, bud formation and leaf senescence are shown above the graph. Daily minimum temperature data are from the Christman Field Weather Station (Colorado Climate Center) about 1 km from the common garden.

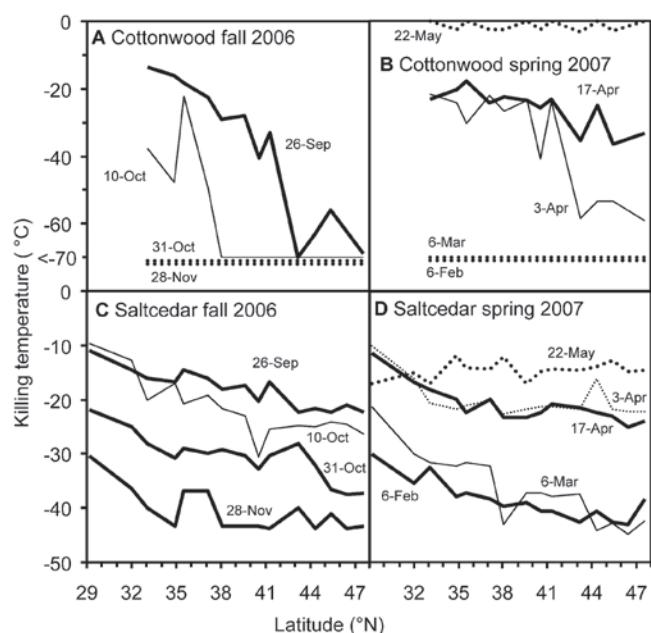


Figure 2. Latitudinal variation in killing temperature for twigs of plains cottonwood during (A) fall 2006 and (B) spring 2007, and saltcedar during (C) fall 2006 and (D) spring 2007. Each line represents data collected on a single date. Solid lines indicate that the effect of latitude was significant at the 0.05 level in multiple logistic regression (dotted lines are not significant). Line and dot thickness are varied arbitrarily for clarity. Plant collection locations are shown in Friedman et al. (2008).

for saltcedar gradually decreased, reaching a minimum in mid-winter. Saltcedar from latitudes 34.9 and 47.6°N survived temperatures of -41°C and -46°C on 12 February 2008. In contrast, killing temperatures decreased precipitously for cottonwood. By mid-October 2007 cottonwood from both 34.9 and 47.6°N latitude survived -70°C, the coldest temperature attainable in our temperature chamber. Temperatures of -70°C or warmer did not kill cottonwood again until April 2008 (Figure 1).

Both cottonwood and saltcedar demonstrated inherited latitudinal variation in cold hardiness (Figure 2). In saltcedar, northern populations survived colder temperatures than southern populations throughout the cold season (Figure 2, C & D). The difference in killing temperature for the extreme latitudes on the gradient (29.2 and 47.6°N) reached a maximum of 15 to 20°C in the spring and fall and decreased to about 10°C in mid-winter (Figure 2, C & D). For cottonwood the latitudinal effect was manifested as a difference in the timing of a critical threshold in fall and spring. Cottonwoods from all latitudes had similar killing temperatures in the summer, underwent a period of rapid cold hardening, and by mid-winter could survive temperatures colder than any that occur in the study region.

Discussion

Although cottonwood is extremely cold hardy in mid-winter, it is less hardy than saltcedar in the late spring and late summer. Leaf flush in cottonwood coincided with a sharp decrease in cold hardiness. This sensitivity to cold in spring may explain the late leaf flush of cottonwood relative to saltcedar. Plains cottonwood leaf buds from several sites across Nebraska opened after those of three other dominant trees in the western Great Plains, *Ulmus americana*, *Fraxinus pennsylvanica*, and *Acer negundo*, and at the same time as those of *Quercus macrocarpa* (McMillan 1957). Therefore, although cottonwood is extremely hardy in mid-winter, sensitivity to cold after

leaf flush limits the growing season for this species.

As predicted, we found strong inherited variation in fall, but not spring, leaf phenology of cottonwood as a function of latitude of origin (Pauley and Perry 1954, Ying and Bagley 1976). In the field, between latitudes 34.9 and 47.6°N, the date of leaf flush of *Populus deltoides* is delayed by about 44 days and the date of growth cessation is advanced by about 32 days (Kaszakurewicz and Fogg 1967). In our common garden, comparing cottonwood populations from latitudes 34.9 and 47.6°N, leaf flush was unaffected by latitude and the date of growth cessation was advanced by an average of 27 days. These results support the hypothesis that the latitudinal variation in fall leaf phenology observed in the field has a strong genetic component related in part to variation in the critical photoperiod for growth cessation, while the latitudinal variation observed in the field in spring phenology is largely a plastic response to the temperature gradient (Friedman and others 2011).

In spite of its recent introduction to North America, saltcedar showed latitudinal variation in the timing of leaf senescence and cold hardiness from fall through spring. Furthermore, growth chamber experiments comparing northern and southern saltcedar have demonstrated inherited temperature-dependent differences in root-shoot ratio (Sexton and others 2002). This latitudinal genetic variation appears to have resulted from (1) multiple introductions of genetically distinct populations, including *T. chinensis* in the south and *T. ramosissima* in the north (Gaskin and Kazmer 2009); (2) hybridization that produced a population containing extensive genetic variation for leaf phenology and cold hardiness (Friedman and others 2008); and (3) natural selection. The hypothesis that the observed latitudinal gradient in North America resulted, at least in part, from natural selection after introduction is supported by the fact that North American *Tamarix* are genetically distinct from Eurasian *Tamarix* (Gaskin and Kazmer 2009).

Summary

In mid-winter, all plains cottonwoods survived colder temperatures than occur in the range of this species, suggesting that exposure to extreme cold in mid-winter is not an important mortality factor. In contrast, saltcedar, even when completely hardened off, was killed by temperatures around -40°C, which is within the temperature range of the northern Great Plains. We conclude that winter cold is a significant factor influencing distribution of saltcedar in the U.S. Increases in winter low temperatures could promote northward spread of saltcedar in the future.

Whereas leaf phenology in our common garden varied with latitude of origin in fall but not spring, cold hardiness of cottonwood and saltcedar twigs varied with latitude of origin in both fall and spring. For a given latitude, the onset of cottonwood cold hardiness occurred after growth cessation and before leaf senescence, and there was strong correlation among growth cessation, leaf senescence, and fall cold hardiness within and between years.

Global increases in temperature could promote earlier leaf flush in spring and later growth cessation and leaf senescence in fall. Our results suggest that cottonwood and saltcedar can accomplish earlier leaf flush through plasticity. To the extent that growth cessation is controlled by photoperiod, however, development of later growth cessation will involve migration and natural selection. The development of a phenological cline in introduced saltcedar is evidence that such change can occur in a shrub population within 150 years.

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