

NOTE

CONSTRAINTS ON WILLOW SEEDLING SURVIVAL IN A ROCKY MOUNTAIN MONTANE FLOODPLAIN

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Abstract: To identify potential constraints on willow (*Salix* spp.) seedling establishment in montane riparian communities in Rocky Mountain National Park, Colorado, USA we established a controlled experiment to examine the effects of soil texture and elevation above river stage on willow seedling survival. We followed seedling survival rates over two summers in paired coarse- and fine-textured plots established at three elevations on study area point bars. Patterns of seedling survival changed over the course of the study, and after two growing seasons, greater seedling survival rates were observed in fine-textured plots and plots occurring at high and intermediate elevations. Our results indicate that both soil water availability and scour by spring floods influence the spatial and temporal patterns of willow seedling survival on point bars along small-order montane streams.

Key Words: *Salix*, safe sites, flood scour, desiccation, Rocky Mountain National Park

INTRODUCTION

Willows (*Salix* spp.) are the dominant woody plant species in many montane riparian areas throughout the Holarctic (Ellenberg 1998, Patten 1998). The general requirements for seedling establishment in the *Salicaceae* are well-described (Moss 1938, Karrenberg 2002), and many studies have examined factors controlling willow and cottonwood seedling establishment (Scott et al. 1996, Mahoney and Rood 1998, Cooper et al. 1999, Dixon et al. 2002). However, most previous studies have been conducted on relatively large rivers, and there is little information available regarding controls on willow seedling survival along small-order montane streams. A better understanding of the factors governing willow seedling survival can help managers identify potential constraints on the natural recovery or restoration of degraded riparian communities and to predict vegetation responses to anthropogenic and natural disturbances, such as large floods and climate change.

Water availability is a principal resource constraining riparian woody plant establishment in arid and semi-arid regions (Sacchi and Price 1992, Ma-

honey and Rood 1998, Cooper et al. 1999), although nutrient availability may also be important under certain conditions (Adair and Binkley 2002). While mature riparian willows are typically phreatophytes, rooting to the water table (Busch et al. 1992, Alstad et al. 1999), it may take several years for seedlings to develop roots long enough to reach the late summer water table (Cooper et al. 1999), during which time, they are prone to water stress and death due to desiccation (Sacchi and Price 1992). Soil texture may also influence seedling survival patterns by controlling soil water-holding capacity and plant-available soil water following floods or precipitation events (McBride and Strahan 1984, Cooper et al. 1999). In lower topographic positions on floodplains, erosion due to floods and ice jams may result in high seedling mortality rates (Scott et al. 1997, Johnson 2000), thereby influencing spatial patterns of plant recruitment. In this study, we analyzed the influence of two factors, soil texture and relative elevation, on patterns of willow seedling survival along a relatively degraded, small-order montane stream.

METHODS

Study Area

Research was conducted in Horseshoe Park (elevation ~2,600 m), a low-gradient, glacial valley located on the east slope of Rocky Mountain National Park (RMNP), Colorado, USA. Fall River, a second-order alluvial stream, flows east through the site and is characterized by a strongly meandering, pool-riffle morphology. Streamflow is unregulated, with the annual, snowmelt-driven peak discharge typically occurring in late May or early June. Mean annual precipitation is ~35 cm, and the study area frequently experiences late-summer monsoonal thunderstorms (Western Regional Climate Center, Estes Park station #052759, 1948–2001). Peak discharge measured at the nearby Big Thompson River gage (USGS gage #06733000) was 63% and 57% of the long-term average in 2000 and 2001, respectively, reflecting regional drought conditions. Summer (June–August) precipitation in 2000 and 2001 was also below normal (83% and 74% of average).

Several willow species, including *Salix monticola* (Bebb), *S. geyeriana* (Andersson), *S. bebbiana* (Sargent), *S. drummondiana* (Barratt), and *S. planifolia* (Pursh), dominate the floodplain, along with wet and dry meadows dominated by herbaceous plant species, such as *Juncus arcticus* (Willdenow) and *Carex utriculata* (Boott). The westernmost portion of Horseshoe Park is relatively undisturbed and supports dense, tall willow communities. The density and stature of willows decreases from west to east, likely due to the impacts of historical agriculture and recreational development, deeper water tables resulting from declining beaver populations, and current high winter elk densities (Peinetti et al. 2002).

Experimental Analysis of Willow Seedling Emergence and Survival

We established a replicated 2×3 factorial experiment on six randomly located, unvegetated point bars to test the effects of soil texture and elevation above the stream channel on seedling emergence and survival over two growing seasons. During the first week of July 2000, following the peak annual discharge, replicate pairs of 0.25-m² plots were established at elevations of 30, 55, and 80 cm above the current stream stage using a laser level. One plot in each pair was established on the native coarse sand and gravel soils, while soil in the other plot was excavated to a depth of ~30 cm and replaced with a loamy fine sand excavated from nearby cut banks and backwaters. Based on work conducted by Woods (2001) on a similar RMNP stream, we assumed that the water-table ele-

vation under point bars approximately equaled stream stage.

We broadcast seeds of the predominant willow species in the study area, *Salix monticola*, at a density of ~300 seeds/m² to ensure homogeneity of seed rain to all plots, and misted each plot daily with ~500 ml of water for one week to encourage germination. Heavy-gauge wire exclosures were placed around plots to limit elk herbivory and trampling. Willow seedlings were tallied in the third week of July and the first week of September during 2000 and the second week of June and the second week of September 2001. Repeated measures ANOVA using the MIXED procedure in the SAS statistics package (SAS Institute 2002) was used to analyze seedling data. Seedling counts were log-transformed to satisfy better the assumption of equal variance for ANOVA. Differences between individual treatment means were compared following a Tukey-Kramer multiple comparisons adjustment.

RESULTS

In late July 2000, plot seedling densities ranged from 0 to 230 seedlings/m². Despite seed and water applications, we observed no germinants in the high elevation coarse-textured plots. Mean mortality from July to September 2000 for all plots combined was greater in high elevation plots (34%) than either intermediate (28%) or low (13%) ones. However, by June of 2001, the pattern was reversed due to the scouring of low elevation plots by spring floods, which killed 96% of the seedlings (Figure 1). After two summers, high elevation fine-textured plots experienced the lowest overall mortality rate (43%). Although seedling mortality rates were greater in the intermediate elevation fine (81%) and coarse-textured plots (90%) than high elevation fine-textured plots, the intermediate elevation plots had higher mean seedling densities on all sampling dates due to higher initial seedling emergence rates (Figure 1). Fixed effect tests for date, texture, and elevation, as well as all two-way interactions (Table 1) were significant.

DISCUSSION

Our results suggest that low soil water content, influenced by elevation above the water table and soil texture, constrain seedling emergence and survival on point bars along montane streams. That willow seedlings failed to establish in our high elevation coarse-textured plots despite the application of seed and water suggests that low soil water holding capacity limits seedling emergence on these sites to years with the highest summer water tables. In addition, the higher seedling mortality rate in high and intermediate ele-

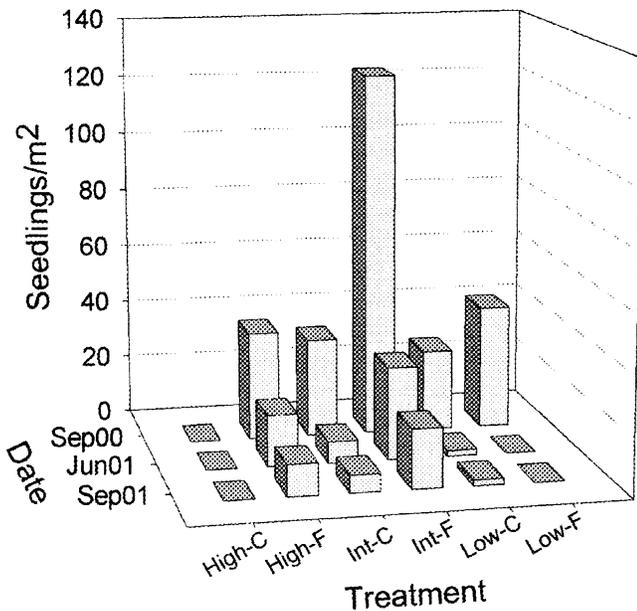


Figure 1. Mean seedling density in study plots in September 2000, June 2001, and September 2001 ($n = 6$). Treatment abbreviations are: HIGH-C = high elevation, coarse texture; HIGH-F = high elevation, fine texture; INT-C = intermediate elevation, coarse texture; INT-F = intermediate elevation, fine texture; LOW-C = low elevation, coarse texture, and LOW-F = low elevation, fine texture.

vation plots during the first summer suggests that soil water availability is an important factor limiting early seedling survival. Sacchi and Price (1992), working on an Arizona floodplain, and Woods (2001), working on a subalpine floodplain in Rocky Mountain National Park, both demonstrated that low soil water content was a primary cause of mortality within willow seedling cohorts.

The relative success of seedlings in our fine-textured high elevation plots demonstrates the importance of soil texture on seedling survival and suggests that the presence of fine textured sediments may ameliorate the risk of water stress and seedling desiccation in locations with deeper summer water tables. This is consistent with results from a study of cottonwood seedling establishment in western Colorado, where seeds germinated across a range of elevations and soil textures, but seedlings survived only in sites with fine-textured soils (Cooper et al. 1999).

Our results also demonstrate that shear forces created by floods affect patterns of willow seedling mortality. Johnson (2000) found that sedimentation and erosion associated with summer flood pulses were a major cause of willow and cottonwood seedling mortality along the Platte River in Nebraska, while Dixon (2003), in a study of the Wisconsin River, found that high winter, spring, and summer flows following in-

Table 1. Results of repeated measures ANOVA from experimental seedling survivorship plots ($n = 6$). Main treatment effects are texture (fine, coarse), elevation (low, intermediate, high), and date (September 2000, June 2001, September 2001).

Effect	DF	F statistic	P value
Texture	1	22.95	0.0003
Elevation	2	5.81	0.013
Date	2	47.71	<0.0001
Texture*Elevation	2	14.66	0.009
Texture*Date	2	6.53	0.004
Elevation*Date	4	10.11	<0.0001

tial seedling establishment caused high levels of seedling mortality. Although mature willows are generally tolerant of moderate flood disturbance (Karrenberg et al. 2002), young seedlings, which lack well-developed root systems, are significantly more vulnerable to flood erosion (Levine and Stromberg 2001).

Along montane streams, our findings suggest that only a small portion of any point bar can meet a seedling's requirements for adequate soil water availability and protection from flood erosion and sediment deposition and that the distribution of such sites is spatially and temporally variable, driven largely by the magnitude and frequency of floods. The timing of annual peak flood stage relative to willow seed rain influences the availability of substrates for seed germination, water availability for developing seedlings, and exposure to shear stresses during floods (Mahoney and Rood 1998, Levine and Stromberg 2001, Amlin and Rood 2002, Dixon 2003). Large intra- and inter-annual streamflow variability, typical of many small-order, unregulated rivers, may limit successful establishment in most years, creating episodic recruitment patterns (Baker 1990, Scott et al. 1997).

Willow seedling-survival patterns observed on point bars may provide insights into processes governing seedling survival on two additional fluvial landforms producing bare and wet soils in our study area: beaver ponds and abandoned stream channels. Beaver dams may gradually fail following abandonment (Meentemeyer and Butler 1999), exposing accumulated fine-textured sediment suitable for seed germination and maintaining relatively stable high water tables conducive to seedling survival. Because of lower stream energy in abandoned channel reaches, seedlings may have reduced mortality risks in subsequent flood events. In contrast, active point bars are exposed to high-energy floods and are typically composed of coarse-textured sand, gravel, and cobble soils; although the most abundant landform in the study area, they may be the least favorable to long-term willow seedling survival.

Although streamflow patterns, principally driven in

many headwater streams by snow pack water content and melt rate, are a primary control on patterns of willow seedling survival, additional factors such as summer precipitation events and the presence of beaver dams may influence the edaphic and hydrologic conditions important for willow seedling survival and recruitment. Even without other limitations on seedling establishment, such as low seed rain density or intense herbivory, changes in hydrologic and geomorphic processes, whether due to reduced beaver populations or climate change, may limit future willow establishment.

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