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NOTE

CO-LIMITATION OF FIRST YEAR FREMONT COTTONWOOD SEEDLINGS BY NITROGEN AND WATER

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Abstract: Nutrient availability strongly affects the species composition and productivity of most upland ecosystems, but the importance of nutrient availability is largely undefined for riparian ecosystems in semi-arid regions of the western United States. The establishment and persistence of riparian cottonwood (*Populus* spp.) seedlings depends largely on water availability, but this does not preclude an important role for nutrient availability. To investigate how nitrogen availability may influence the composition and productivity of riparian communities, we tested the hypothesis that the growth and survival of first-year Fremont cottonwood seedlings is limited by the availability of both water and nitrogen. Plots of naturally germinated cottonwood seedlings along the Yampa River in Northwest Colorado were randomly assigned one of four treatments: control, water, nitrogen, or water plus nitrogen. Additions of nitrogen or water doubled total (root plus shoot) seedling and shoot length. Water additions did not increase root growth, while N addition doubled the root extension of first-year cottonwood seedlings. The water-plus-nitrogen treatment doubled total seedling and root length, and tripled shoot length. Additions of water or nitrogen also more than doubled cottonwood seedling survival through the first growing season. This co-limitation of cottonwood germinants by both water and nitrogen suggests that the productivity and species composition of riparian vegetation may need to be examined in relation to supplies of resources other than water.

Key Words: seedling growth, resource limitation, nitrogen, water, *Populus deltoides*, riparian

INTRODUCTION

Nutrient availability strongly affects the species composition and productivity of most upland ecosystems (Aber and Melillo 1991), but in semi-arid ecosystems, water has historically been considered the primary control on these characteristics (Noy-Meir 1973, Sala et al. 1988). Water availability also plays a strong role in controlling the community composition and productivity of semi-arid riparian ecosystems (Scott et al. 1996, Poff et al. 1997, Begg et al. 1998, Smith et al. 1998), but the importance of nutrients (especially nitrogen) in regulating these ecosystem characteristics remains largely unexplored. Given the evidence for co-limitation of semi-arid upland ecosystems by water and nitrogen (Lauenroth et al. 1978, Seastedt and Knapp 1993, Hooper and Johnson 1999) and the relative availability of water in riparian areas in semi-arid climates, nitrogen availability could play an important part in controlling the productivity and species composition of semi-arid riparian ecosystems.

The overstories of western semi-arid forested riparian ecosystems are generally dominated by cottonwood (*Populus*) species, so determining what controls cottonwood growth and establishment is crucial to maintaining these ecosystems. Cottonwood seedlings are strongly limited by the availability of soil water and light, and first-year cottonwood seedling mortality is typically attributed to desiccation or shading (Scott et al. 1996, Begg et al. 1998, Cooper et al. 1999). Susceptibility to desiccation may be due to limited development of root systems, as cottonwood seedling roots must grow rapidly downward to remain connected to a receding floodplain water table (Chapin 1993, Scott et al. 1996, Taylor et al. 1999).

The role of nutrients (particularly nitrogen) in regulating the establishment and growth of cottonwoods remains largely undefined. Specifically, if nutrient supply regulates cottonwood seedling root growth when water and light are abundant, greater nutrient availability might result in faster root extension. This could allow the seedling to maintain contact with the steadily dropping floodplain water table and enable the seedling to continue to acquire water and nutrients that are not provided by the germinant's small seed (Pallardy and Kozlowski 1979, Chapin 1993). Increased root growth could therefore promote cottonwood establishment by allowing the root to maintain contact with soil water for a longer period of time during the first growing season, by decreasing the typical 3–5 year period before which cottonwood trees maintain constant contact with the water table (become phreatophytic), and/or by increasing water-use efficiency (Chapin 1993, Pregitzer and Friend 1996).

To examine resource limitation on the productivity of semi-arid riparian areas, we tested the hypothesis that the growth and survival of first-year Fremont cottonwood seedlings (*Populus deltoides* subsp. *Wislizenii* (Watson) Eckenwalder) is limited not only by soil water availability, but also by the availability of soil nitrogen.

METHODS

This study was conducted in northwestern Colorado, USA on the floodplain of the Yampa River in Deerlodge Park in Dinosaur National Monument. Deerlodge Park is a wide, alluvial valley at an elevation of 1705 m. The Yampa River is a relatively unregulated river with a snowmelt-driven hydrology. Mean annual discharge is 58 m^3 s^{-1}, with a mean annual instantaneous peak of 400 m^3 s^{-1} in the spring and a mean annual base flow of 12 m^3 s^{-1} (Merritt and Cooper 2000). The floodplain along the Yampa River in Deerlodge Park is vegetated by Fremont cottonwoods with a wide range of age classes, abundant willow (*Salix* spp.), and only small amounts of tamarisk (*Tamarix ramosissima* Ledeb.). Young soils are fluvial Entisols (E. F. Kelly, personal communication). Textures of deposited sediments in the study area ranged from sand to clay deposited in layers, with sandy loam and loamy sand the most common. The nearest weather station, located approximately 35 km east of Deerlodge Park in Maybell, Colorado, has a recorded mean annual temperature of 5.5° C and mean annual precipitation of 280 mm.

Cottonwood seedlings germinated during the last week of June 1998. The experiment was installed along two aggrading meanders in Deerlodge Park on July 7, 1998, when seedlings were still less than 4 cm in height. We randomly located 15 sites in areas with naturally germinated cottonwood tree seedlings and established plots at these sites in a two-factor randomized block design with 15 blocks and four treatments per block. Blocks of four 1 m^2 plots (one per treatment) were established at each of the 15 sites. We marked the four corners of each plot and a 50×50 cm area in the center of each plot with 30-cm-long steel stakes. Each 1×1-meter plot was randomly assigned one of four treatments: control, water, nitrogen, or water plus nitrogen.

The nitrogen treatment consisted of a one-time addition of 5 g N m^{-2} as ammonium nitrate fertilizer applied in dry form and crushed into the soil in early July. The mean level of available nitrogen (ammonium and nitrate) in control plot soils was 0.079 g N m^{-2}. Water treatments consisted of 2.5 cm of river water applied once every 5–7 days from July 7 to September 19, 1998. A total of 33 cm of water was applied to each water or water-plus-nitrogen treatment plot. Concentrations of ammonium and nitrate in river water were very low compared to both our addition rate and levels of available ammonium and nitrate in the soil. Eight samples of river water had concentrations of N in ammonium and nitrate between 0.0 and 0.2 mg N L^{-1}. Long-term data (1973–1993) for the Yampa River near Maybell, Colorado are consistent with these data, with average concentrations of 0.06 and 0.38 mg N L^{-1} in ammonium and nitrate (USGS 2000).

The 50×50 cm area in the center of each plot was monitored weekly; we counted the total number of live seedlings and recorded the apparent cause of death of the seedlings located in this 50×50 cm area. Most seedling deaths appeared to result from desiccation or herbivory by cottonwood leaf beetles (*Chrysomela scripta* Fabricus).

On September 19–20, 1998, at the end of the growing season prior to leaf fall, the five largest seedlings from the 50×50 cm area in the center of each plot were excavated. We dug a 1.5-m trench in front of the selected seedlings and carefully excavated the five seedlings by hand. We measured the aboveground and belowground length of each seedling.

Five of the seedling blocks sustained extensive damage from cottonwood leaf beetle herbivory, including extensive (>90%) defoliation, stunted growth, and death. These blocks were all located in one section of the floodplain. Each block contained all four treatment types, and all treatments suffered from extensive herbivory. These blocks were omitted from data analyses and results.

We performed an analysis of variance (ANOVA) on the root, shoot, and total (root plus shoot) lengths using the following independent variables: water, nitrogen, block, and all first order interactions (SAS Version 8.0). The null hypothesis was that first-year cottonwood seedling growth and survival are not limited by nitrogen or water.

RESULTS

Total, root, and shoot mean seedling lengths all increased in the following order: control < water only or nitrogen only < water + nitrogen (Figure 1). Additions of nitrogen or water doubled total seedling length and shoot length, supporting the hypothesis that seedling growth is limited by both N and water avail-

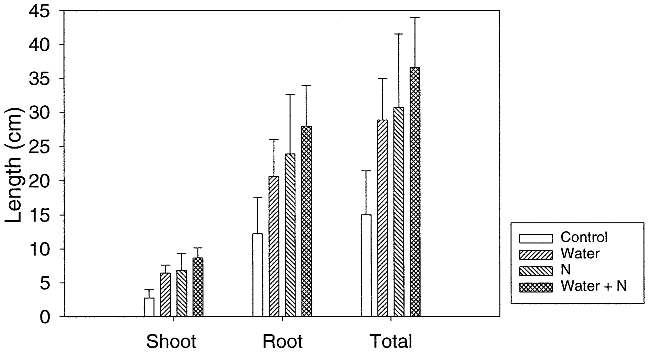

Figure 1. Mean lengths of cottonwood seedling shoots, roots, and entire seedlings. Error bars are 1 standard error of the mean.

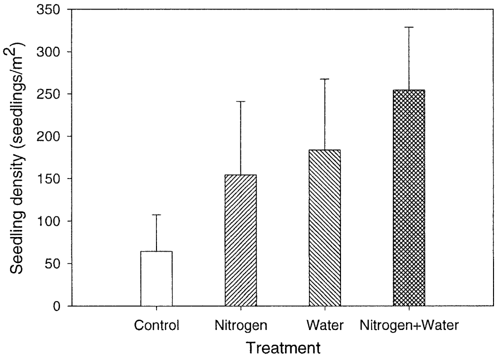

Figure 2. Seedling densities (seedlings/m²) ± SE for each treatment at the end of the growing season (day 76).

ability. Root length for watered seedlings averaged 8 cm longer than control roots, but the effect was not significant (Table 1). Nitrogen fertilization doubled the root extension (an average of 12 cm longer) of first–year cottonwood seedlings. The interaction between water and nitrogen was not significant. On average, additions of water plus nitrogen more than doubled total and root growth and tripled shoot growth (Table 1).

Seedling density was not controlled in the experiment, and natural thinning of seedlings occurred. Seedling density at the end of the growing season was greatest in the nitrogen plus water treatments (Figure 2). Additions of water nearly tripled seedling survival, and nitrogen fertilization more than doubled seedling survival through the growing season (Table 2).

All seedling lengths increased with seedling density ($P < 0.0001$). If intraspecific competition controlled seedling length, the plots with the greatest seedling densities would have the shortest lengths. Our data shows the opposite trend, suggesting that resource availability, not intraspecific competition, limited cottonwood seedling growth.

DISCUSSION

For the last century, the classic idea of a single limiting resource has dominated the study of limiting resources and ecosystem management (Sprengel 1828, Liebig 1840). However, field experiments with natural plant communities have shown plant productivity and species composition to be limited, either chronically or intermittently, by multiple resources (Lauenroth et al. 1978, Seastedt and Knapp 1993, Hooper and Johnson 1999). Our results support the idea of limitation by multiple resources by demonstrating that first–year cottonwood seedling growth and survival is limited by both nitrogen and water.

Although our experiment did not investigate whether the nitrogen and water limitation of seedling growth was chronic or intermittent, it is likely that nitrogen availability affects seedling growth most strongly at times during the growing season when water is plentiful. The establishment of cottonwood seedlings depends on germinants maintaining contact with the water table as river stage declines (Segelquist et al. 1993, Braatne et al. 1996, Begg et al. 1998, Cooper et al. 1999). The availability of nitrogen during times when water is not limiting could be essential in determining rates of root growth. For seedlings without access to

Table 1. Summary of analysis of variance for cottonwood seedling growth. Sample size (n) is ten.

		Shoot				Root				Total			
	df	MS	*F*	*P*	R²	MS	*F*	*P*	R²	MS	*F*	*P*	R²
Model	30	37.34	3.66	0.022	0.924	490.95	2.31	0.093	0.885	755.25	2.69	0.060	0.899
Block	9	79.77	7.83	0.003		1091.51	5.14	0.011		1617.56	5.77	0.008	
Nitrogen	1	99.92	9.81	0.012		894.6	4.22	0.070		1378.25	4.92	0.054	
Water	1	75.50	7.41	0.024		387.26	1.82	0.209		970.25	3.46	0.096	
Water*N	1	7.94	0.78	0.401		47.71	0.22	0.647		156.40	0.56	0.474	
Block*Water	9	14.9	1.42	0.304		208.53	0.98	0.510		336.95	1.20	0.394	
Block*N	9	9.82	0.96	0.521		188.73	0.89	0.568		284.68	1.02	0.491	
Error	9	10.1				212.2				280.41			

Table 2. Summary of analysis of variance for cottonwood seedling density at the end of the first growing season. Sample size (n) is ten.

		Seedling density			
	df	MS	*F*	*P*	R^2
Model	30	4170.49	3.92	0.018	0.929
Block	9	10601.34	9.98	0.0011	
Nitrogen	1	4020.03	3.78	0.0836	
Water	1	7535.03	7.09	0.0259	
Water*Nitrogen	1	60.03	0.06	0.8175	
Block*Water	9	1038.36	0.98	0.5135	
Block*Nitrogen	9	971.36	0.91	0.5521	
Error	9	1062.69			

sufficient nitrogen, root growth may be unable to keep up with dropping water tables. This could result in either reduced growth or death.

The potential role of nitrogen as a co-limiting resource in riparian ecosystems means that microsite conditions and anthropogenic changes in patterns of N availability in riparian ecosystems could potentially affect riparian community composition and productivity. Our results suggest that nitrogen-enriched microsites or increases in nitrogen availability from anthropogenic inputs (e.g., atmospheric deposition or agricultural runoff) or invasive N-fixers such as Russian olive (*Elaeagnus angustifolia* L.) will facilitate the initial growth and survival of Fremont cottonwood seedlings.

Despite the results of this experiment, it remains unclear how increases in available nitrogen would affect Fremont cottonwood growth, establishment, and ultimately riparian species composition in the face of interspecies competition. Increased N availability has changed the species composition of a variety of ecosystems by altering competitive relationships between species (Lauenroth et al. 1978, Wedin and Tilman 1996, Vitousek et al. 1997). In some cases, increased N availability has led to the dominance of one or a few N-responsive or demanding species and declines in species adapted to infertile soils (Heil and Diemont 1983, Tilman 1987, Vitousek et al. 1997).

Cottonwood seedlings are adapted to growth in nutrient-poor environments (Johnson 1992, Scott et al. 1997). Increased levels of available nitrogen could alter community composition by changing the competitive relationship between cottonwood and other species, such as non-native tamarisk. The effects of increasing nitrogen availability on the competitive relationship between cottonwood and tamarisk are unknown.

Maintaining southwestern riparian ecosystems depends on understanding how available nitrogen affects riparian community composition and interspecies competition, especially with exotic species. Further research on nutrient cycling in riparian ecosystems should clarify linkages between nutrient availability and plant community composition and productivity.

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