

RECLAMATION

Managing Water in the West

Nitrogen Effects in Western Riparian Areas

**Research and Development Office
Science and Technology Program
Final Report 2014-0015**



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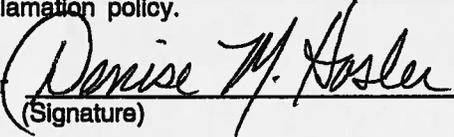
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Disclaimer

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Executive Summary

Restoration of riparian productivity lost as a consequence of flow regulation is a common management goal in dryland riverine ecosystems. In general, Nitrogen (N) limits plant productivity in mesic environments, whereas water limits productivity in semiarid and arid regions (drylands). Included in these plant groups are both floodplain trees such as *Populus*, which are fast-growing, nutrient-demanding trees and herbaceous floodplain plants. In this study we examined both tree and herbaceous vegetation response to N fertilization along dryland rivers. Because trees are phreatophytic in drylands, and have water needs met in whole or in part by a shallow water table, their productivity could be limited by N availability. We added 20gN m⁻² in a 2-m radius around the base of mature *Populus fremontii* along each of a regulated and free-flowing river in semiarid northwest Colorado, USA (total $n = 42$) in order to test whether tree growth was constrained by low soil N. Twelve years after fertilization, we collected increment cores from these and matched unfertilized trees and compared radial growth ratios (growth in the 3-year post-fertilization period/growth in the 3-year pre-fertilization period) in paired t tests. We expected a higher mean ratio in the fertilized trees. No effect from fertilization was detected, nor was a trend evident on either river. An alternative test using analysis of covariance (ANCOVA) produced a similar result.

We also performed an N-fertilization experiment on two floodplains to directly test whether herbaceous productivity was N-limited and used commercial ion-exchange membrane probes to examine N supply rates *in situ* at several desert riparian sites in the Colorado River Basin. We assessed the usefulness of this technology and initiated an evaluation of N-limitation in dryland riparian herbaceous communities. Cation- and anion-exchange probes deployed for up to 6 months indicated great variability in N supply rates. Probe nitrate levels were highly correlated with nitrate levels in soil collected when probes were retrieved, and total probe N correlated with an estimate of productivity, suggesting that probe N levels can provide a meaningful index of site-specific N limitation. We failed to detect a fertilization effect, but several lines of indirect evidence suggested productivity was N limited at some sites.

Our results underscore the need for additional assessment of which and to what extent factors other than water control dryland riverine productivity. Positive confirmation of adequate soil nutrients at these and other dryland riparian sites would bolster the argument that flow management is necessary and sufficient to maximize productivity and enhance resilience in affected desert riverine forests. The nature of N-limitation in dryland riparian zones and its implications with respect to community dynamics and management deserve further attention.

INTRODUCTION

Reclamation has interests in riparian restoration projects which are typically related to water delivery, water salvage, or avoiding impacts to endangered species. Reclamation is supporting restoration projects on several rivers in the west and a large amount of money has been directed towards these restorations. Over \$1 billion dollars has been spent just in the Southwest since the 1980's. Restoration is largely used to ensure that Reclamation can continue to supply users with water and power, often via trade of restoration for water. There is little information on riparian zone nutrient dynamics in the semiarid and arid western US, despite its great importance to ecosystem structure and functioning. This gap in understanding of dryland riverine ecosystems constrains water and land management options. We examined the hypothesis, generated from an array of empirical studies, that desert riparian vegetation is generally limited by soil nitrogen (N). We included manipulative (fertilization) landscape-scale experiments in two contrasting river basins with an assessment of N in restoration site riparian soils and foliage to address the importance of N in limiting productivity and determining the community composition of riparian vegetation. Dryland riparian areas may be characterized by low plant-available N. The low plant-available soil N results from low N inputs and the relatively slow recycling of organic N through decomposition/ mineralization, which is itself co-limited by local weather and the flow regime. Understanding the consequences of N-limitation remains a key knowledge gap on riparian plants and other biota. A greater understanding of N controls on dryland riparian systems will enhance the ability of water resource managers to adaptively manage restoration projects.

METHODS

We addressed questions critical to understanding the importance of N in western riparian ecosystems and interactions with the flow regime. We focused on ecologically important western plant species, including Fremont cottonwood (*Populus fremontii*), an obligate riparian tree. We also examined the N-response of herbaceous vegetation found along floodplains. We tested the hypothesis that growth of mature riparian vegetation is widely limited by low soil N. This was tested in several ways. First, we collected and analyzed tree growth data from mature cottonwood trees that received N fertilizer in 1999. A total of 78 trees were fertilized in 10 locations at Deerlodge Park on the unregulated Yampa River and 92 were fertilized in 10 locations at Browns Park on the highly regulated Green River. Near each fertilized tree a matched unfertilized control was located. We compared tree growth before and after fertilization for each tree, thus letting each tree serve as its own control. Second, we studied herbaceous plant response in the field, to determine whether vegetation is N-limited. We established pairs of matched plots containing representative herbaceous vegetation at both Deerlodge Park and Browns Park. We randomly selected plots from each pair for treatment and added N. Adding 15 g N m⁻² represented doubling the amount of N

mineralized annually in Browns Park. To estimate mineralization rate (MR) over the growing season, we added a Plant Root Simulator probe (PRSTM) to each of the plots at each site. At the end of the growing season, we retrieved the PRSTM probes, clipped vegetation in each plot to determine total aboveground biomass, and subsampled foliage to determine foliar N concentration (FN). We also documented MR at locations from the Lower Colorado using PRSTM probes.

RESULTS

More in depth methods and results are presented in Appendices A and B.

Appendix A: JOURNAL ARTICLE

RESEARCH ARTICLE

Can Nitrogen Fertilization Aid Restoration of Mature Tree Productivity in Degraded Dryland Riverine Ecosystems?

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Abstract

Restoration of riparian forest productivity lost as a consequence of flow regulation is a common management goal in dryland riverine ecosystems. In the northern hemisphere, dryland river floodplain trees often include one or another species of *Populus*, which are fast-growing, nutrient-demanding trees. Because the trees are phreato-phytic in drylands, and have water needs met in whole or in part by a shallow water table, their productivity may be limited by nitrogen (N) availability, which commonly limits primary productivity in mesic environments. We added 20 g N m⁻² in a 2-m radius around the base of mature *Populus fremontii* along each of a regulated and free-flowing river in semiarid northwest Colorado, USA (total $n = 42$) in order to test whether growth is constrained by low soil N. Twelve years after fertilization, we collected increment cores from these and matched unfertilized trees and compared

radial growth ratios (growth in the 3-year post-fertilization period/growth in the 3-year pre-fertilization period) in paired t tests. We expected a higher mean ratio in the fertilized trees. No effect from fertilization was detected, nor was a trend evident on either river. An alternative test using analysis of covariance (ANCOVA) produced a similar result. Our results underscore the need for additional assessment of which and to what extent factors other than water control dryland riverine productivity. Positive confirmation of adequate soil nutrients at these and other dryland riparian sites would bolster the argument that flow management is necessary and sufficient to maximize productivity and enhance resilience in affected desert riverine forests.

Key words: cold desert, Colorado, environmental constraints, floodplain, Fremont cottonwood, growth, nutrient, *Populus*, tree rings.

Introduction

Riverine forests in the world's semiarid and arid regions (drylands) are threatened by flow regime changes linked to river regulation, increasing human demands for water, and climate change (Tockner & Stanford 2002; Andersen et al. 2007; Mac Nally et al. 2011; Perry et al. 2012). In the northern hemisphere, these forests often contain one or another species of *Populus*, fast-growing trees that have a high nutrient demand (Heilman et al. 1996; Misra & Tewari 1999; Van Den Driessche et al. 2008). The potential for hydrologic shifts to stress riparian *Populus* is well documented (Scott et al. 1999; Monda et al. 2008; Singer et al. 2012), but stressors can interact and managing resilience to one stress, e.g. reduced water availability,

requires understanding what other stressors are actually or potentially present. Nutrient deficiency, especially inadequate nitrogen (N), may be present in dryland riparian ecosystems, particularly where alluvium is coarse-textured. Sand is typically nutrient-poor, and sandy sediment may contain few nutrients and little organic matter to serve as a source of N.

Low N availability limits productivity in many terrestrial environments (Vitousek & Howarth 1991), and N has been suggested to limit productivity in riverine ecosystems of the desert Southwest (Schade et al. 2002). Dryland riparian *Populus* are obligate phreatophytes, and N availability may be constrained by the combination of low inorganic N concentrations in alluvial sediments, in surface water and groundwater (Grimm & Fisher 1986a; Schade et al. 2005), and slow N mineralization rates in riparian soils (Schade et al. 2002; Adair et al. 2004; Andersen & Nelson 2006). Where dryland riparian *Populus* or other tree species are N-limited, fertilization might offer managers a tool for restoring lost ecological productivity or improving individual tree resilience to stress from factors operating now or in the future.

In the southwestern United States, dryland riparian forests are usually dominated or co-dominated by *Populus fremontii* S. Wats. (Fremont cottonwood), a foundation species (Ellison et al.

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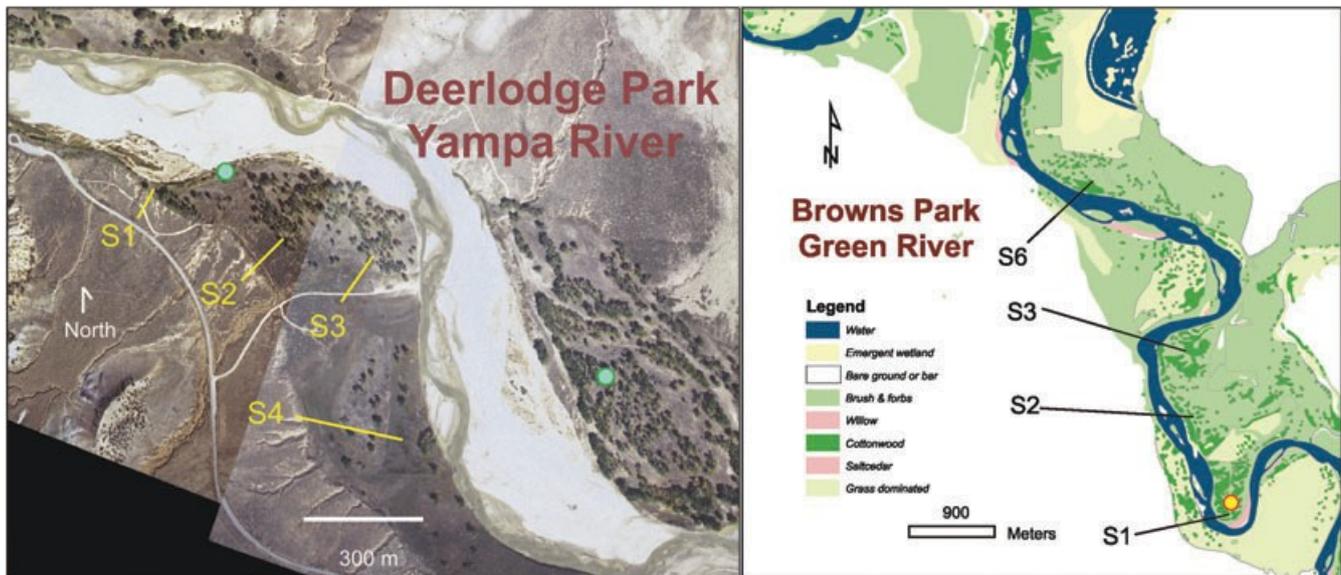


Figure 1. The Deerlodge Park (DLP; Yampa River) and Browns Park (BP; Green River) study areas, showing locations of the subsites containing the study trees. Flow in the Yampa River is from right to left; Green River flow is from left to right. The two dots at DLP and single dot at BP are locations where microclimates and ground water levels were monitored.

2005; Stella et al. 2011) of widespread conservation interest. We tested the hypothesis that productivity of mature *P. fremontii* is N-limited in a fertilization experiment conducted on two floodplains in northwest Colorado. Nitrogen deficiency is known to restrict *P. fremontii* seedling growth on one of the floodplains (Adair & Binkley 2002). At these locations, *P. fremontii* is near its distributional limit in the Colorado River Basin. If nutrient deficiency is a factor determining that distributional limit, mature trees at these sites may be especially sensitive to nutrient supplementation by fertilization.

Methods

Study Areas and Experimental Design

We worked along sand-bedded segments of the Green River in Browns Park National Wildlife Refuge and the Yampa River in Dinosaur National Monument. These rivers originate in the Rocky Mountains and each is characterized by a snowmelt-driven spring flood. The study areas, about 75 km apart, are alluvial floodplains that feature similar semiarid climates: Deerlodge Park (DLP; elevation approximately 1,705 m) on the Yampa River and Browns Park (BP; elevation approximately 1,635 m) on the Green River above its confluence with the Yampa. The river flow patterns at DLP and BP were quite similar prior to the 1963 closure of Flaming Gorge Dam on the Green River (Cooper et al. 1999). Mean annual discharge of the Green River at BP and the Yampa River at DLP were approximately 58 and ~ 55 m³/s, respectively, with flood peaks typically ranging between 400 and 600 m³/s. Tight regulation of Green River discharge in the BP reach has eliminated overbank flows, which has in turn altered floodplain ground water dynamics and nutrient cycling (Adair et al. 2004; Andersen & Nelson 2006).

The floodplain forest at both DLP and BP is monotypic *Populus fremontii*. The patches of mature trees typically feature an open canopy, with total cover less than 50% and often much less (Fig. 1). Williams and Cooper (2005) systematically measured canopy light interception along transects through stands of mature trees at both DLP and BP and reported 27–48% of PAR intercepted at BP and approximately 60% at DLP. Intraspecific competition for light among these trees is possible, but probably minor. Details concerning climates and soils are available in Cooper et al. (1999), Adair et al. (2004) and Williams and Cooper (2005).

An irruption of defoliating cottonwood leaf beetles (*Chrysomela scripta* F.) occurred at DLP during the study period (Andersen & Nelson 2002; Andersen 2005). Beetles first became apparent in 1997 and possibly peaked in abundance in 2001. The defoliation level in mature trees is unknown. Beetle abundance dropped precipitously during the summer of 2002, with individuals very rare by autumn. The beetles were consistently rare at BP.

We systematically selected study trees from multiple locations on each floodplain, with the intention of having two sets of trees at each subsite, matched by size, to serve as treatment and control groups. There were four subsites at DLP (Fig. 1), three of which (S1, S2, and S3) were along a surface inundated every decade or so. Stand density varied, with highest density at S2 and S3. Trees ranged from approximately 60 to 100+ years old. The topographically highest subsite (S4) contained scattered, very large cottonwoods (>150 years old; Fig. 1).

The Browns Park trees were also selected from four subsites. The oldest trees (>60 years old) were at S1, S2, and S6 and the youngest trees at S3 (Fig. 1). The latter included trees from the only post-dam era cohorts, generated in 1969, 1984, and 1986 (Cooper et al. 2003). Herbaceous cover at the BP

subsites was variable, but generally lighter than at DLP. Trees on both floodplains were marked with numbered metal tags nailed through the bark. Half of the study trees, systematically chosen to ensure dispersion of treated and control trees within each subsite, were fertilized with granular ammonium nitrate in January 1999 at a rate of 20 g N m^{-2} around the base of each tree (2-m radius). This rate (200 kg N ha^{-1}) is common in forest nutrition studies for large trees, such as lodgepole pines (Binkley et al. 1995) and has been shown effective in mesic-region cottonwood nutrition studies (DeBell et al. 1975).

We used a 25-cm three-thread Suunto increment borer to collect a 5-mm core (occasionally two) from each tree that could be relocated in mid-March 2012 (late winter). Cores were dried, mounted, and sequentially sanded to 600 grit (approximately 25 micron) following Cooper et al. (2003). Ring borders were delineated and ring widths measured (0.01 mm precision) using a binocular microscope and measuring stage with a linear encoder and digital readout device. We plotted a ring-width series for each core and compared series within and among trees. Cross-dating was principally, but not entirely, based on unusually narrow rings produced in years featuring rare, extremely low flood discharge. Ring series that showed shifts in all or part of the chronology were double-checked for missing rings or undetected borders, often after resanding. All dendrochronological analyses were completed without knowledge of a tree's treatment class.

We hypothesized that the cottonwoods are N-limited, and predicted an increase in radial growth in response to N fertilization. We quantified this expected increase in two ways. First, we calculated for each tree a ratio (R_G) of the 1999–2001 cumulative growth increment (the three growing seasons after fertilization) to the 1996–1998 cumulative growth increment (the three growing seasons before fertilization). Regardless of other environmental factors within a subsite that might be affecting tree growth, e.g., local groundwater depth and dynamics or insect herbivory, we expected R_G to be greater, on average, in the fertilized tree group.

By comparing R_G values, we circumvented the potential problem of variation among trees in their radial growth rates; each tree effectively served as its own control. We assume within-tree age-trend (the decrease in annual ring width with tree age, given constant annual volume increment, due to the annual increase in ring diameter) can be ignored because we pair trees by size. Variability in growth rates is to be expected at all spatial scales, due to variability in phenotypes, local soil stratigraphy, topographic position, distance to the river channel, and other factors. Our second method of quantifying the predicted increase in growth rate addressed the potentially confounding effects from size and spatial variability in a different manner, and allowed us to include fertilized and unfertilized trees excluded from the above analysis because they lacked a matching tree for pairing. In an examination of growth patterns in the decade prior to fertilization, we documented a strong linear relationship between the annual radial increment in a year featuring relatively benign-to-favorable environmental conditions (1996, the year prior to the beetle irruption at DLP) and the total (or mean) increment during the seven prior years (Fig. 2). This

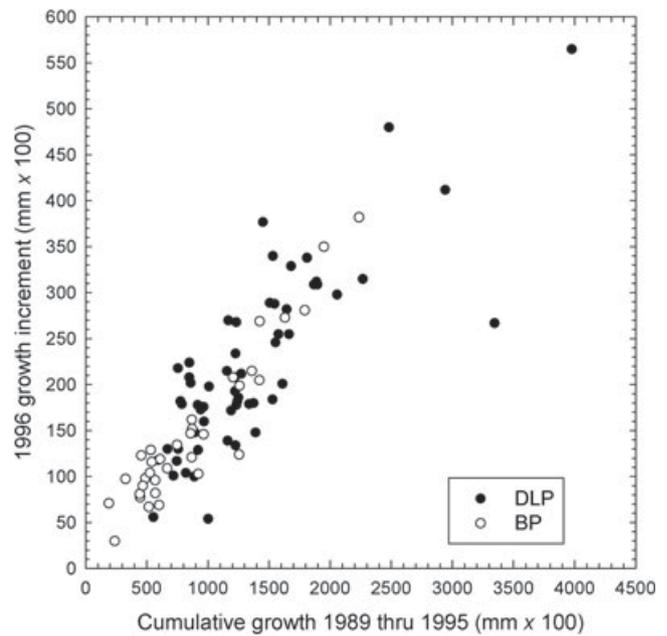


Figure 2. Scatterplot showing the linear relationship ($p < 0.001$, $r^2 = 0.76$) between a Fremont cottonwood tree's level of growth in 1996 (a representative "non-stressful" growing season) and its cumulative (or mean) growth in prior years, here the seven previous growing seasons. Patterns for Deerlodge Park (DLP) and Browns Park (BP) trees are not significantly different (ANCOVA interaction term $P = 0.10$). Note that 1996 is prior to both the initiation of the fertilization experiment (January 1999) and the eruption of defoliating leaf beetles at Deerlodge Park (DLP).

relationship supports the assumption that a tree's mean annual growth during a period in the recent past is a good predictor of annual growth in future years, given similar (non-stressful) growing conditions. Given this assumption, we related growth during the 3-year (1999–2001) post-fertilization period (G_S) to a 10-year pre-fertilization period. We expected to see a slope in the relationship between G_S and cumulative growth in the 10-year pre-treatment period for fertilized trees that was steeper than the slope in the relationship for unfertilized trees.

Efficacy of Fertilizer Application Method

We conducted an experiment at DLP in 2013 to assess the efficacy of surface application of dry N fertilizer to supply N to mature *P. fremontii*, whose roots lie below those of potentially competing understory herbaceous plants. We established two parallel 50-cm by 200-cm plots, separated by 150 cm, under a mature tree at four locations within the S1 and S2 subsites (Fig. 1). We fertilized one plot in each pair with granular urea at the rate of 20 g N m^{-2} . We used urea because ammonium nitrate is no longer commercially available. We evaluated the plant-available nitrogen supply rate during the growing season using in-situ (buried) ion-exchange membranes in a commercial product, Plant Root Simulator (PRS™) Probes (Western Ag Innovations, Saskatoon, Saskatchewan, Canada). This well-established technique (Hangs et al. 2004) is based on the adsorption of NO_3^- (and other anions) from the soil solution

onto an ion-exchange membrane prepared to adsorb anions, and NH_4^+ (and other cations) onto a membrane prepared to adsorb cations.

We installed three pairs of PRS probes at each of two depths (“shallow” and “deep”) in each plot. We installed shallow probes in pairs approximately 25, ~100, and ~175 cm from one end of the plot. Each pair consisted of a cation-exchange probe and an anion-exchange probe separated by approximately 15 cm and installed such that the membrane contacted soil from approximately 5–10 cm below the mineral soil surface. Deep probe pairs consisted of one anion probe and one cation probe attached to a single drop-line, with a 1-cm thick clay “spacer” placed between their lower tips to separate the inner membrane surfaces. We lowered each pair into a hand-augered hole so that the membranes were at approximately 60 cm depth, then backfilled the holes with excavated material in a manner to approximately restore the original soil stratigraphy. Soil aggregates were broken up prior to backfilling and the backfilled material lightly tamped periodically to eliminate voids. The drop-line, which extended to approximately 10-cm above the surface, was left in place to mark the location of the probes. We added fertilizer to the treatment plot immediately after probe installation on 9–10 May 2013.

We retrieved probes after approximately 124 days exposure, on 10–11 September. We immediately cleaned each probe of adhering soil using deionized water and kept the probes cold and moist until shipped cold to the manufacturer for analysis. The three probes of each type were pooled for plot-level analysis. We used the sum of plot-level PRS-NO_3^- and PRS-NH_4^+ values to index total plant-available nitrogen supplied during the exposure period (PRS-N).

Data Analyses

We used a one-tailed paired t test at each subsite to test the hypothesis that there was a positive difference between R_G values in fertilized and unfertilized trees. The separate tests provided a means to detect variability in fertilization effects that might be due to local (subsite) soil conditions or inundation frequency. We subsequently pooled data as appropriate to increase sample sizes and statistical power, and repeated the paired t test at each site. We paired treatment and control trees within subsites by matching them according to their radial increment in 1996, a year close to the date of fertilization but prior to the herbivorous beetle irruption at DLP. Both total annual and summer precipitation in 1996 were above average (Maybell station), flows were not unusual (see Results), and we found no evidence in the ring series to suggest that tree growth was restricted at either DLP or BP. We ranked the trees in each group by ring width, then paired ranks starting with trees with the largest rings. At subsites where the number of trees in each group was unequal, we shifted pairings if it produced a closer size match. Two fertilized and 12 unfertilized trees for which there was no match were excluded from the analysis.

Our second test method, which ignored subsites within floodplains, allowed us to assess whether a fertilization effect was present and if so, whether it differed between BP and DLP. We

used a two-factor analysis of covariance (ANCOVA) to compare G_S of fertilized and non-fertilized trees at BP and DLP, using the cumulative 10-year (1989–1998) growth increment prior to fertilization as the covariate. We first tested whether the required assumption of homogeneity of group slopes was met by examining whether there was an interaction between the treatment and the covariate. The subsequent ANCOVA allowed us to include all trees for which we had complete data for the 1989–2001 period, including the 14 trees not used in the paired t tests.

We tested for effectiveness of the fertilizer application using one-tailed paired t tests. We expected to see higher plant-available N in fertilized plots compared to control plots, at both shallow and deep depths, and performed separate tests for effects on PRS-NO_3^- , PRS-NH_4^+ , and Total PRS-N.

Results

Fremont Cottonwood Tree Rings

Both DLP and BP cottonwoods showed strong variation in annual increments, reflecting year-to-year variation in environmental conditions (Fig. S1, Supporting Information). Not all ring series were judged satisfactory in terms of readability; we used the ring series from 34 of 39 BP trees and 59 of 63 DLP trees in the statistical analyses.

River Hydrology and Floodplain Microclimates

Below-average flood flows characterized the first 4 years of the pre-fertilization period (1989–1998) at DLP (Fig. S2). However, some very large floods occurred in the years preceding fertilization, with all DLP subsites inundated in 1997. The post-fertilization 1999 flood did not inundate any of the DLP subsites, and subsequent floods in 2000 and 2001 were even smaller. Flow patterns at BP, including controlled spring flood flows, varied throughout the study period (Fig. S2), from a year with almost no flood (1990) to several years with modest floods (capped at dam power plant capacity, approximately $130 \text{ m}^3/\text{s}$) mimicking the natural hydrograph. The 1997 and 1999 floods were exceptionally large, involving releases at full power plant capacity plus use of other outlet works (bypass tubes and spillway). Although these high flows raised the BP floodplain water table to levels not seen since the early 1980s, it is unclear whether any BP subsite was inundated.

The first post-fertilization (winter) quarter of 1999 featured average precipitation, but April and May were very wet, leading to a spring much wetter than average (Fig. 3). Summer precipitation was also above average.

Effects of Fertilization on Tree Growth

We failed to detect an effect from fertilization at any subsite (Table 1), and the fertilization effect based on the pooled subsite data was far from significant at both BP and DLP ($p \geq 0.23$; Table 1). The mean growth ratio (R_G) of fertilized trees averaged 6% greater than unfertilized trees along the Green River and 4% less than unfertilized trees along the Yampa River. Mean

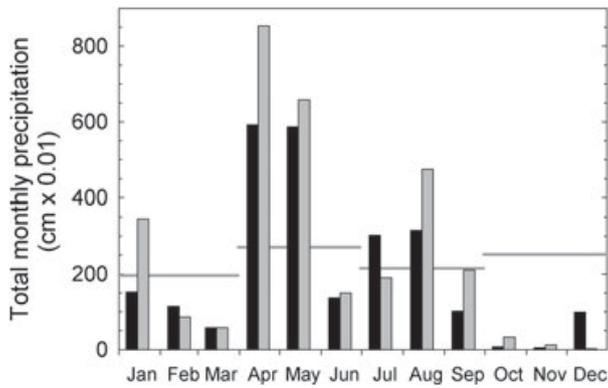


Figure 3. Total monthly precipitation during 1999 at Deerlodge Park on the Yampa River (DLP; dark vertical bars) and Browns Park on the Green River (BP; light vertical bars), and the long-term quarterly average for DLP (horizontal lines). Long-term quarterly values for BP would be slightly lower. The monthly data cover the first growing season after the fertilizer was applied in January 1999. Monthly data are from microclimate monitoring stations established at each site (Fig. 1). Quarterly means are based on records for the National Weather Service’s Maybell, CO station (20km from DLP).

Table 1. Results of one-tailed paired *t* tests comparing ratios of post-fertilization growth to pre-fertilization growth (R_G) in fertilized and non-fertilized mature Fremont cottonwood, matched by general size (DBH class) and width of the 1996 growth ring, at Browns Park (BP) on the regulated Green River and Deerlodge Park (DLP) on the unregulated Yampa River.

Floodplain	Subsite	Mean R_G value		<i>t</i>	<i>df</i>	<i>p</i>
		Unfertilized	Fertilized			
BP	S1	1.174	1.166	-0.084	2	0.530
	S2	0.891	1.062	1.214	3	0.156
	S3	0.804	0.933	1.264	5	0.131
	S6	1.065	0.870	-0.957	2	0.780
DLP	S1	0.538	0.535	-0.029	7	0.511
	S2	0.564	0.554	-0.142	6	0.554
	S3	0.663	0.606	-1.072	6	0.838
	S4	0.848	0.842	-0.060	3	0.522
BP	pooled	0.944	0.997	0.767	15	0.228
DLP	pooled	0.638	0.615	-0.568	26	0.713

R_G values within subsites were generally lower at DLP than at BP (Table 1).

Similarly, no effect from N fertilization was detected in radial growth of trees at either DLP or BP using growth during the 10-year period prior to the date of fertilization to standardize subsequent growth. Following confirmation of homogeneity of slopes (Fig. 4), ANCOVA comparing the 3-year cumulative post-treatment growth increment for fertilized and non-fertilized trees, with the 10-year cumulative pre-treatment growth as a covariate, indicated no treatment effect at either location (DLP: $p = 0.13$; BP: $p = 0.20$). ANCOVA performed on the pooled data, again with the 10-year cumulative pre-treatment growth as a covariate, indicated no effect from fertilization ($p = 0.82$; Table 2), but suggested the possibility of a river effect ($p = 0.08$) on post-1998 growth.

Efficacy of the N Application Technique

Fertilization increased total PRS-N levels in both shallow and deep soils (Table 3). Mean total PRS-N concentration at the 60-cm depth was raised by 75%, primarily due to a 300% increase in PRS- NO_3 availability in the fertilized plots (Fig. 5).

Discussion

The failure to find a fertilization effect on radial growth at any subsite at either DLP or BP was surprising, and can be interpreted several ways. First, the lack of an effect could mean that growth of mature trees is not N-limited. Although N-limitation is mentioned in floodplain plant literature (Follstad Shah & Dahm 2008; Nielsen et al. 2010), few studies have addressed N-limitation in natural riparian plant communities. Walker and Chapin (1986) experimentally showed that addition of NPK fertilizer increased productivity of tree seedlings, including *Populus balsamifera*, on early successional sites within an Alaska floodplain. Adair and Binkley (2002) found addition of N increased both root extension and survival of first-year Fremont cottonwood seedlings naturally established on the DLP floodplain. N is considered to be limiting in Southwestern desert streams and their floodplains, but this generalization stems from only a few datasets (Grimm & Fisher 1986b). Total soil N increased at a relatively rapid rate of 3 to 8 g N m⁻² yr⁻¹ in chronosequences at DLP and BP (Adair et al. 2004), but whether the higher N levels are adequate to meet mature tree needs has not been established. Furthermore, the formation of mycorrhizas (Beauchamp et al. 2006) may lead to different requirements in seedlings and mature trees.

An alternative explanation for our result is that the trees are N-limited, but the fertilizer dose was too small or the application needed to be repeated in multiple years to elicit the expected response. As noted earlier, the dose we applied is commonly used in forest nutrition studies for large trees. Smaller doses applied annually over many years can in some cases provide a greater growth response than a single large dose (cf. van Miegroet et al. 1994; Hogberg et al. 2006). The cottonwoods we fertilized may have shown a response in a non-measured productivity trait, such as root biomass or reproductive output. It

is also possible that one or more mechanisms restricted fertilizer-N uptake by the trees, precluding removal of the N-limitation and increases in growth. Precipitation was generally below average in the winter months immediately following fertilization, but well above average in spring, when herbaceous plants would be greening up. Thus, conditions may have favored the added N remaining on or near the soil surface and dilution or removal by spring precipitation or, alternatively, uptake by shallow-rooted understory plants (Warren et al. 1986) or immobilization in soil microbial biomass. Our application efficacy experiment demonstrated that surface application of N fertilizer can increase plant-available N in deep soils on the DLP floodplain, at least in some years, but conditions at the time of tree fertilization could not be precisely duplicated. Tree uptake of N at DLP could also have been restricted if leaf beetle defoliation disrupted root functioning (Kosola et al. 2001). Given some

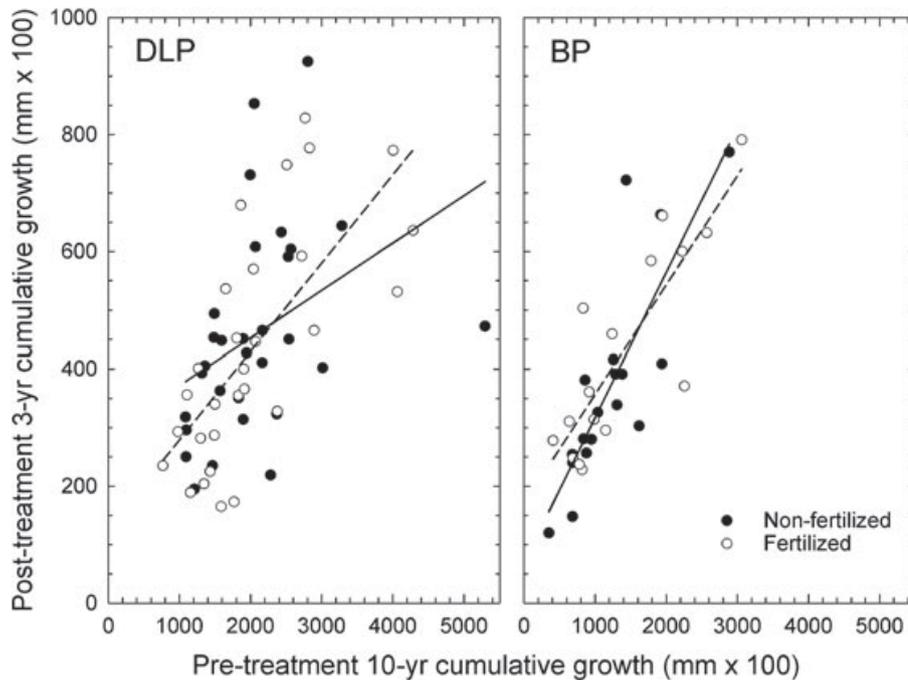


Figure 4. Total radial growth for fertilized (open circles) and non-fertilized (filled circles) trees at Deerlodge Park (DLP) and Browns Park (BP) over the three growing seasons following fertilization (1999–2001) plotted against the total growth over the 10 growing seasons prior to fertilization (1989–1998). The slopes of the least-square regression lines for the fertilized (dashed line) and non-fertilized (solid line) trees are not significantly different at either location (ANCOVA, treatment \times 10-year growth interaction; DLP: $p = 0.15$, BP: $p = 0.26$).

Table 2. Results of ANCOVA performed on the 3-year cumulative post-treatment growth increment for treated (fertilized) and control (non-fertilized) trees on the Deerlodge Park (Yampa River) and Browns Park (Green River) floodplains.

Source	Sum of squares	df	Mean square	F-ratio	P
Treatment	1136.0	1	1136.0	0.055	0.815
River	64858.2	1	64858.2	3.129	0.080
Covariate	1207619.2	1	1207619.2	58.255	0.000
Treatment \times River	14662.6	1	14662.6	0.707	0.403
Error	1824220.3	88	20729.8		

The 10-year cumulative pre-treatment growth was used as a covariate.

level of N uptake by DLP trees, the lower R_G value in the fertilized rather than the unfertilized trees at DLP could be explained by the beetles preferentially defoliating fertilized trees (Athey & Connor 1989). The generally lower R_G values at DLP compared to BP and the trend toward a river effect in the ANCOVA likely reflect an overall adverse effect on growth by the defoliating beetles, which were present solely at DLP (Andersen & Nelson 2002). Given these multiple possibilities for restriction of fertilizer uptake by the BP and DLP trees, and the potential for confounding effects from leaf beetle herbivory, we consider our results suggestive rather than conclusive regarding N-limitation in mature trees on these floodplains.

In summary, our data suggest, but do not conclusively show that mature *Populus fremontii* are not N-limited at our study sites. Water availability is commonly considered the primary

Table 3. Results of one-tailed paired t tests assessing whether urea fertilization increases plant-available total inorganic nitrogen (N), nitrate (NO_3), and ammonium (NH_4) levels, as measured by ion-exchange PRS probes in deep and shallow soils under mature Fremont cottonwoods on a dryland floodplain ($df = 4$ in all cases).

Soil depth	Nitrogen form	t	p
10 cm	Total PRS-N	-2.511	0.043
	PRS- NO_3	-1.520	0.113
	PRS- NH_4	-8.063	0.002
60 cm	Total PRS-N	-3.126	0.026
	PRS- NO_3	-3.385	0.021
	PRS- NH_4	-0.989	0.198

factor limiting growth in dryland riparian trees (Reily & Johnson 1982; Stromberg & Patten 1996; Robertson et al. 2001; Rood et al. 2003; Andersen 2005), but the mechanisms linking local hydrology and productivity remain unclear and interactions among limiting resources are likely (Liu & Dickmann 1993; Adair & Binkley 2002). Soil nutrients other than nitrogen, e.g., phosphorus (Lewis et al. 2010), may also limit productivity on these floodplains. Our negative results underscore the need for additional assessment of which and to what extent factors other than water control dryland riverine productivity and ecosystem resilience. Before dismissing N fertilization as a practical management option to increase cottonwood productivity in degraded systems or to enhance resilience in dryland riparian ecosystems, additional testing using different application rates is warranted. Positive confirmation of adequate soil N at

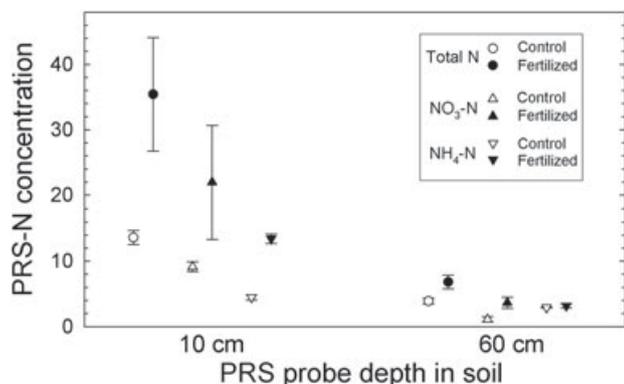


Figure 5. Mean (± 1 SE) inorganic nitrogen concentrations on PRS probes exposed from May to September at two soil depths (10 and 60 cm) in four sets of paired fertilized and unfertilized plots on the Deerlodge Park (DLP) floodplain. Units are μg nutrient/ 10 cm^2 ion-exchange membrane surface area. Values are for nitrate (PRs- NO_3), ammonium (PRs- NH_4), and their sum (PRs-N).

these and other dryland riparian sites would bolster the argument that flow management is necessary and sufficient to achieve high levels of productivity in degraded desert riverine cottonwoods.

Implications for Practice

- Restoring dryland riverine forest productivity lost as a result of reduced soil water availability, or increasing resilience of established restoration tree plantings to water stress in dryland riparian areas, may be achievable through nitrogen fertilization.
- Until future studies reveal general patterns, local testing for soil nutrient constraints on tree productivity is needed to inform managers about the efficacy of fertilization as a means to enhancing productivity of degraded dryland riparian forest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Unadjusted ring width series for a random selection of 10 Browns Park (BP) and 10 Deerlodge Park (DL) Fremont cottonwoods included in the study. The marker year 1963 is denoted by the vertical solid line in the BP plots, whereas the 1976 marker year is denoted in the same manner in the DL plots. The shaded box in each plot denotes the study period years 1989–2001. All plots are drawn at the same scale.

Figure S2. Hydrographs showing the annual flood pulses on the free-flowing Yampa River at Deerlodge Park (thin green line) and the regulated Green River in Browns Park (heavy blue line) from 1989 to 2001. All plots are to the same scale and show daily mean discharge from 23 February through 20 August. Data are from USGS gages 09260050 (Yampa River at Deerlodge Park, CO) and 09234500 (Green River near Greendale, UT), respectively. For 1995 and 1996 and some earlier years when the Deerlodge gage was inoperative, flows at DLP are estimated as the sum of upstream gages 09251000 (Yampa River near Maybell, CO) and 09260000 (Little Snake River

Appendix B: DRAFT JOURNAL ARTICLE

Does nitrogen limit dryland riparian plant productivity?

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Abstract

Nitrogen (N) commonly limits plant productivity in mesic environments, whereas water limits productivity in semiarid and arid regions (drylands). Plants in riparian zones along rivers in drylands are less likely to be water-limited, and thus their productivity may also be limited by N. We used commercial ion-exchange membrane probes to examine nitrogen (N) supply rates *in situ* at desert riparian sites in the Colorado River Basin (southwestern USA) to assess the usefulness of this technology and begin an evaluation of N-limitation in dryland riparian communities. We also performed an N-fertilization experiment on two floodplains to directly test whether herbaceous productivity was N-limited. Cation- and anion-exchange probes deployed for up to 6 months indicated great variability in N supply rates. Probe nitrate levels were highly correlated with nitrate levels in soil collected when probes were retrieved, and total probe N correlated with an estimate of productivity, suggesting that probe N levels can provide a meaningful index of site-specific N limitation. We failed to detect a fertilization effect, but several lines of indirect evidence suggested productivity was N limited at some sites. The nature of N-limitation in dryland riparian zones and its implications with respect to community dynamics and management deserve further attention.

INTRODUCTION

Plant-available soil nitrogen (N) commonly limits primary productivity in mesic environments, whereas water is the dominant factor controlling productivity in drylands (Fenn et al. 2003). Desert river floodplains, however, have a relatively shallow water table that provides water to phreatophytic vegetation, suggesting floodplain productivity in deserts may be primarily N-limited. Riverine riparian soils commonly develop on landforms generated through deposition of fluvial sediment. In the

southwestern USA, these sediments commonly include sand derived from sandstones and igneous rocks exposed in the headwater and middle reaches of rivers. Sand is typically nutrient-poor, and sandy sediment may contain few nutrients and little organic matter (OM) to serve as a source of N. Nitrogen-fixing plants can add N to riparian soils, but these plants are uncommon in many southwestern dryland riparian zones. Thus, dryland riparian sites that are sandy, with little OM, no N-fixing plants, and little or no anthropogenic N input ([Fenn et al. 2003](#)) are likely to be nutrient-poor. Not all vegetation on desert floodplains is phreatophytic, however, and these shallow-rooted species may rely on precipitation to meet their moisture requirements. These plants may also be N-limited when moisture supplies are adequate. Where productivity of phreatophytic desert riparian vegetation is N-limited, fertilization may offer a means to increase resilience to stress resulting from hydrologic change brought about by flow management or climate change. Fertilization may also improve plant growth and survivorship in desert riparian restoration efforts.

In this paper we address several questions concerning N availability to plants and N-limitation in desert riparian vegetation. First, we examine soil attributes and an index of soil N availability at four widely separated floodplain locations in drylands of the Colorado River Basin in order to characterize N dynamics and begin to understand how flow regime and water quality might influence the inorganic N supply. All locations harbored native floodplain plants, including Fremont cottonwood (*Populus fremontii*), although one had undergone extensive restoration/rehabilitation efforts. We ask whether N supply rates are comparable to those found in other riparian and dryland environments. We expected to find nitrogen supply levels to be low except in the case of the restored floodplain, where there were potential N inputs associated with both the restoration effort and effluent-dominated stream flows. We also expected to find low levels of soil organic matter, and correspondingly low soil total N in the natural floodplains. Secondly, we use an N-fertilization experiment on two of the floodplains to test the hypothesis that herbaceous productivity is N-limited.

STUDY AREAS

We examined multiple sites along dryland segments of four rivers in the Colorado River Basin, which drains much of the southwestern USA. Two streams, Las Vegas Wash (LVW) and the Bill Williams River (BWR), are in a warm-desert environment, and two, the Green and Yampa rivers, are in a cold-desert environment (Figure 1; Table 1). Flow in the LVW is dominated by municipal wastewater treatment plant effluent ([Andersen and Nelson 2013](#)), but it also carries stormwater runoff generated in the Las Vegas, Nevada metropolitan area. The latter can raise discharge levels by an order of magnitude and more. Severe channel-bed degradation and bank erosion has occurred over the past 50 years ([Duan and Scott 2007](#)), and the segment examined here has been the focus of channel rehabilitation and floodplain revegetation efforts.

Large upstream dams affect the discharge of the entire Bill Williams River ([Shafroth et al. 2010](#)) and the segment of the Green River where we worked, Browns Park (BP) ([Cooper et al. 1999](#)). We worked in Deerlodge Park (DLP) on the Yampa River. Yampa River flows are affected by only small dams and diversions, with the result that the annual hydrograph at DLP is nearly natural ([Cooper et al. 1999](#)).

We varied the landforms examined at each location. Three sites were established along LVW, two under mature Fremont cottonwoods in relatively fine-textured sandy soils and one under coyote willow (*Salix exigua*) in a soil dominated by coarse sand and fine gravel. Two of the three sites established at BWR were on relatively high surfaces under the edge of a Fremont cottonwood and Goodding willow (*Salix gooddingii*) stand (BWR1), whereas the third was under such a canopy at a relatively low position (BWR2). Two of the six sites established at BP were in sparse vegetation under widely-spaced mature Fremont cottonwoods in the interior of a meander bend (BP1) where inundation no longer occurs and ground water is rarely within two meters of the ground surface (Table 2). A third site (BP1-Gly) was established on a similarly high surface, but where the clonal N-fixing plant American licorice (*Glycyrrhiza lepidota*) was abundant. The remaining three sites were established in variably dense herbaceous vegetation along the outer margin of a point bar (BP2) in positions relatively close to the water table and possibly subject to inundation during large controlled releases. Two of the five sites established at DLP were on a surface inundated only during very large floods (DLP1) and remainder were under young Fremont cottonwood trees in an area subject to inundation every few years (DLP2). Soils data for the BP, DLP, and BWR sites are presented in Table 3. We have no soils data for LVW (see below).

Although comparative data are lacking, nutrient loads were likely low in three of the four streams, the exception being Las Vegas Wash. LVW waters, because of the effluent they contain, have inorganic N concentrations (sum of NH_4^+ -N and NO_3^- -N) that averaged around 15 mg N/L, compared to total nitrogen (inorganic plus organic N) concentrations at reference stream sites in the xeric western United States range that ranged from 0.22–0.90 mg N/L (Nelson 2011). Twice-yearly samples from the Bill Williams River during 2010-2013 produced values of <0.09 and <0.01 mg N/L, respectively. Bi-monthly samples collected from the Green River near BP during 1998-2000 had an average concentration of ($\text{NO}_3^- + \text{NO}_2^-$) < 0.04 mg N/L. Fifteen samples collected approximately quarterly from the Yampa River at DLP during 2010-2013 had average concentrations of ($\text{NO}_3^- + \text{NO}_2^-$) < 0.12 mg N/L and NH_4^+ < 0.02 mg N/L (<http://nwis.waterdata.usgs.gov/co/nwis/qwdata>).

Discharge within each examined river segment was continuously measured during the study period at a nearby USGS gage (LVW: Las Vegas Wash at Pabco Road near Henderson, NV (# 09419700); BWR: Bill Williams River near Parker, AZ (# 09426620); BP: Green River near Greendale, Utah (# 09234500); DLP: Yampa River at Deerlodge Park, Colorado (# 09260050). We estimated precipitation using data from the closest National Weather Service station except at BP, where we measured daily precipitation on site using a tipping-bucket rain gage and datalogger.

METHODS

Soil plant-available nitrogen supply rate

We evaluated relative rates of plant-available nitrogen supply during the growing season at each river location using in-situ (buried) ion-exchange membranes in a commercial product, Plant Root Simulator (PRS™) Probes (Western Ag Innovations, Saskatoon, Saskatchewan, Canada). This well-established technique (Hangs et al. 2004) is based on the adsorption of NO_3^- (and other anions) from the soil solution onto an ion-exchange membrane prepared to adsorb anions, and NH_4^+ (and other cations) onto a

membrane prepared to adsorb cations. The continuous adsorption simulates uptake of these ions by plant roots (for additional information see: <http://www.westernag.ca/innovations/>). Following exposure to the soil solution for some period, the ion concentration on the membrane provides an index of plant-available nitrogen supplied during that period, and allows comparison of relative supply rates among sites where the probes were deployed.

We assessed N supply in 50 x 200 cm plots, within which we installed three pairs of PRS probes, at ~25, ~100, and ~175 cm from one end of the plot. Each pair consisted of a cation-exchange probe and an anion-exchange probe separated by ~15 cm and installed such that the membrane contacted soil from ~5 to 10-cm below the mineral soil surface. Dates of probe installation and retrieval varied between the warm- and cold-desert locations (Table 2). Retrieved probes were immediately cleaned of adhering soil using deionized water and kept cold and moist until shipped cold to the manufacturer for analysis. The three probes of each type were pooled for plot-level analysis. We used the sum of plot-level PRS-NO₃⁻ and PRS-NH₄⁺ values to index total plant-available nitrogen supplied during the exposure period (PRS-N).

All plots at a site were similar in terms of plant species composition and cover. Plots contained only herbaceous species, although the species mix varied among sites. No plot was protected from herbivores.

Effects of fertilization on herbaceous biomass and N-supply

We tested the hypothesis that herbaceous plants at the cold-desert sites were N-limited by comparing productivity in fertilized and unfertilized plots. At the same time that a plot was installed to measure N supply rate (described above), we installed a second plot parallel to the first and separated from it by 150 cm. PRS Probes were installed in an identical manner, after which the downstream plot in each plot-pair was fertilized using urea [CO(NH₂)₂] pellets (15 g N m⁻²).

The PRS Probes in the fertilized plots were retrieved at the same time as those in the untreated plots (Table 2). At the time of PRS probe retrieval, we also collected a soil sample (0-15 cm depth) from each plot, composited from two points separated by 1 m. No soil was collected from the LVW sites because of the substrate alterations that took place there (see Results). Soil was air-dried in the field and stored in a freezer until shipped for nutrient and texture analysis to the Colorado State University Soil, Water and Plant Testing Laboratory.

Aboveground standing live and dead herbaceous plant material judged to be from the 2012 growing season was clipped from each DLP plot ($n = 30$) on 22-23 October 2012. The equivalent plant material was collected from the BP *Glycyrrhiza* plots ($n = 12$) at the same time, but a snowstorm precluded clipping material in the remaining BP plots ($n = 30$) until early the following spring (27 March 2013). All collected plant material was immediately air-dried and subsequently dried to constant mass (60°C) in the laboratory and total biomass determined. During that spring visit we also collected freshly emergent green herbaceous foliage where it was present in DLP ($n = 1$ plot-pair) and BP ($n = 5$ plot-pairs). Analysis of total nitrogen concentration in this foliage was performed by the Colorado State University Soil, Water and Plant Testing Laboratory.

Statistical analyses

We used the Shapiro-Wilk test to test for normality in the within-site PRS-N data. We used ANOVA followed by Bonferroni pairwise comparisons to compare PRS-N means and test the hypotheses that N supply would be greater in LVW sites than in BWR sites and comparable at DLP and BP. We tested the hypothesis that N supply rate would be greatest in soils where soil OM was highest by using ANOVA to compare PRS-N values among sites within each river segment.

We expected to see an increase in N supply in the fertilized plots compared to control plots. We used 1-sided paired *t*-tests with plots grouped by river and site type to test this hypothesis. We hypothesized that fertilization would result in greater plant growth, and predicted greatest biomass from the fertilized plot in each pair of plots. We used a 1-sided paired *t*-test with sites pooled to compare plant biomass from fertilized and unfertilized (control) plots on each river.

We considered statistical significance at $\alpha = 0.05$. Means are presented as $X \pm 1$ SE.

RESULTS

Climate conditions and hydrology

With the exception of Las Vegas Wash, all sites where PRS probes were deployed likely received less than 5 cm of precipitation during the deployment period (Table 2). Unusually severe, monsoon-related storms produced moderate to heavy rain in the Las Vegas Wash drainage basin. As a result, at least two major flood flows occurred in Las Vegas Wash and fluvial erosion and deposition led to significant geomorphic change at all three sites. We recovered all PRS probes at only one site, where the flood(s) had deposited ~15 cm of coarse sand over the plots. PRS probes were recovered from a single plot at each of the other two sites. In both cases the plots had been buried under ~20 cm of mixed silt, clay, and fine sand.

There was no evidence of flooding at the BWR sites, based on Bill Williams River discharge records and the physical condition of the sites when probes were recovered. An usually large spring flood release led to Green River discharge at the BP sites reaching ~224 m³/s in late May. This discharge may have led to saturated soils at the BP2 sites for a few days, but physical evidence suggested no site was inundated. The peak Yampa River discharge during the 2012 spring flood (169 m³ s⁻¹) was less than half the long-term average (381 m³ s⁻¹), and it is likely that no plot at DLP was inundated.

Nitrogen mineralization as indexed by PRS probes

The PRS-N data fit a normal distribution for 23 of 26 site-location combinations where the Shapiro-Wilk test was possible (i.e., $n \geq 3$). The exceptions were the BP1-*Gly* control plots ($n = 6$) and one set each of BP2 fertilized and control plots ($n = 3$ each). The BP1-*Gly* site contained a single outlier with a PRS-N value double that of the other five plots. Given the preponderance of satisfactory fits, we chose to use parametric statistical tests for all comparisons.

We limit our comparisons of PRS values to locations within each region. Because ion uptake rates on the probe membrane is non-linear, the different probe exposure durations (Table 2) make between-region comparisons inappropriate.

Warm-desert sites.—The loss of plots at two of the three Las Vegas Wash sites led us to pool all LVW plots into a single group. PRS-N values at the two BWR1 sites were strikingly different, although consistent within each site, which led us to treat the two sites as separate groups, BWR1a and BRW1b. Individual plot values ranged from 0.9 to 284, with PRS-nitrate contributing the majority of N in all BWR plots, whereas PRS-ammonium contributed most to PRS-N in three of the five LVW plots. In a comparison of these four warm-desert groups, the N supply rate as indexed by PRS-N was significantly higher at BWR1a than at either of the other two Bill Williams River sites or at the pooled LVW sites (ANOVA: $F = 12.25$; $df = 3, 10$; $P = 0.001$) (Figure 2). Mean values for the latter three groups were not significantly different (Figure 2).

Cool-desert sites.—Individual values of PRS-N in the unmanipulated plots at the cold-desert sites ranged from 2.3 to 83.3. The contribution from nitrate predominated in most plots, with the ratio of the contributions from nitrate to that of ammonium ranging from 0 to 35. The mean ratio was 6.8 (SE = 1.23, $n = 36$). One-way ANOVA indicated no difference in mean PRS-N between BP1 and BP2 at BP ($F = 30.742$; $df = 1, 13$; $P = 0.76$), nor was there a difference between mean PRS-N values at BP1-*Gly* and the pooled BP1 and BP2 sites ($F = 0.998$; $df = 5, 15$; $P = 0.45$). One-way ANOVA comparing PRS-N among locations within grouped sites at DLP indicated a significant difference between DLP1 and DLP2 ($F = 13.015$; $df = 1, 13$; $P = 0.003$). The higher DLP1 sites had a mean PRS-N value more than triple that of the lower landform (Figure 2). A final ANOVA comparing the pooled BP sites to the DLP1 and DLP2 sites indicated no difference in mean PRS-N value between DLP1 and the BP sites (Post-hoc Bonferroni pairwise comparison $P = 0.058$; Figure 2).

The level of herbaceous biomass in an unmanipulated DLP plot was positively related to the plot's PRS-N value (Figure 3 Panel A). However, we were unable to detect such a relationship at either BP1-*Gly* (linear regression: $n = 6$, $P = 0.43$) or the other BP sites ($P = 0.33$).

The PRS-NO₃⁻ values and the NO₃⁻ concentrations in the soil samples (Table 3) were correlated (Pearson $r = 0.68$; $n = 39$; $P < 0.001$) in the pooled regional dataset, as were PRS-N and NO₃⁻ concentrations ($r = 0.71$; $n = 39$; $P < 0.001$). In contrast, PRS-N and soil Total N, which includes N unavailable to plants, were uncorrelated ($P = 0.50$). Mean soil nitrate level at BP1-*Gly*, where N-fixing plants were common, was two to three times greater than levels at BP1 and BP2 (1-way ANOVA: $F = 13.6$; $df = 2, 13$; $P = 0.001$), but not significantly higher than the highest mean level found at DLP, where N-fixing plants were rare (DLP1: 2-sample t -test, $P = 0.56$).

Fertilization experiment

Each set of plot-pairs grouped by topographic position (as in Figure 2) showed the expected effect of greater PRS-N in the fertilized plot (Table 4). The level of increase, as indicated by the mean ratio of values in the fertilized and control plots, varied from a low of 2.1 at BP-*Gly* to 10.8 at BP1 (Table 4). However, because of within-set variability, there was no significant difference among the five groups in the mean ratio for plot pairs (ANOVA: $F = 1.39$; $df = 4, 31$; $P = 0.26$). Nitrate levels increased in 35 of the 36 plot pairs, whereas ammonium increased in about 75% of the plot pairs.

We found no significant fertilization effect on standing crop biomass at BP in either the pooled data ($t = -1.002$; $df = 14$; $P = 0.33$) or at individual sites ($df = 2$ for each test; $P \geq 0.11$). Nor did we find an effect from fertilization on standing crop biomass at DLP ($t = -0.739$; $df = 14$; $P = 0.47$). Further, separate paired t -tests for data collected at each site ($n = 5$) failed to detect an effect at any individual site ($df = 2$ for each test; $P \geq 0.30$). Mean standing crop biomass values varied from a low of 12 g m^{-2} at DLP2 to 113 g m^{-2} at BP1-*Gly* (Figure 4).

A significant positive relationship between plot biomass and PRS-N level was evident in the fertilized plots (Figure 3 Panel B), but the relationship was weaker than that noted in the unfertilized control plots (Figure 3 Panel A). We were unable to detect a relationship between fertilized plot biomass and PRS-N at BP1-*Gly* (linear regression: $n = 6$, $P = 0.62$).

Nitrogen concentration (% N) in fresh green biomass collected in Spring 2013 was on average 27% higher in the fertilized plots (one-sided paired t -test: $t = -2.354$, $df = 4$, $P = 0.039$). The mean concentrations in the fertilized and control plots were $3.5 \pm 0.26\%$ and $2.8 \pm 0.27\%$, respectively.

DISCUSSION

We consider the soil N levels to be low in many, but not all, of our study sites, based on comparison of measured N levels (Table 3) to those of “low fertility” soils described in the literature. For example, Tilman and Cowan (1989) described a soil with a total N concentration of 0.013% as being “extremely nitrogen poor,” and a soil with a total N concentration of 0.18% as N-rich. These authors clearly recognized that total N does not necessarily represent plant-available N, however, and so even a soil with a relatively high total N value could be supporting N-limited plants. One of the factors controlling mineralization and the N supply to plants is soil moisture. Under dry conditions on desert floodplains, mineralization may be hindered in the upper soil even if plants can access moisture in the capillary fringe.

We expected to find plant-available N supply levels to be higher in riparian sites along Las Vegas Wash than in similar sites along the Bill Williams River. This expectation was based on our assumption that the soil nutrients at the LVW sites are coupled to surface water nutrient concentrations, and nutrient concentrations in LVW flows are elevated as a result of wastewater treatment plant inputs. Counter to our expectations, we found LVW values were similar to those at two of the three Bill Williams River floodplain sites (Figure 2), and nowhere near the high values found at the third BWR site.

The very high PRS-N values found at BWR1a suggest conditions there were substantially different from those at the other BWR sites. The three plots making up BWR1a all had high PRS-N values (131, 145, and 285) and in each case the value was due to high nitrate level. The plots were separated by tens of meters, indicating the factors involved were widespread locally, and not, for example, due to an isolated instance of urine deposition. Soil texture at BWR1a was quite similar to that found at the other BWR sites (Table 3). BWR1a plots were located in an opening under the edge of the cottonwood/willow forest canopy and <50 m from perennial surface water, which might have led to the site being preferentially used by a pack of collared peccaries (*Tayassu tajacu*) or other resident wildlife. However, we noted no evidence of animal presence on any plot.

PRS-N levels varied substantially across landforms at the cold-desert locations, with values at Deerlodge Park bracketing those recorded at Browns Park (Figure 2). There was a non-significant trend for higher PRS-N in the Browns Park *Glycyrrhiza* patch than at the other BP locations, which lacked this N-fixing plant. The highest PRS-N values were at DL1, a relatively high, seldom-inundated floodplain meadow with no overhead tree canopy and patches of dense herbaceous vegetation. This site contained scattered Fremont cottonwoods >200 years old, and Adair et al. (2004) documented soil N accumulation through time along both Yampa and Green river floodplains. In contrast, DL2 was a mid-elevation floodplain location, more frequently flooded and plots were generally under young (< 40 yr-old) cottonwoods. Herbaceous plants were sparse in the DL2 plots compared to the DL1 plots (Figure 4), and the species make-up differed.

Differences in hydrology can explain why PRS-N was greater at DLP1 than at BP1, a site harboring large cottonwoods presumably similar in age to those at DLP1. Soil OM and NO₃⁻-N were both greater at DLP1 than BP1 (Table 3). This may reflect the fact that although the ground surface position is relatively high at DLP1, the spring flood moistens surface soils in most years, because the flood-driven rise in the water table is typically large enough to allow capillary action to wet the soil even when no inundation occurs. In contrast, surface soils at BP1 have not been inundated since at least 1984 and in most years are now wet only by direct precipitation, because the depth to the water table remains >1.5 m even during the spring flood release (D. C. Andersen, unpublished data). The relatively large flood release of 2012 led to the depth to the water table decreasing to a minimum of ~0.8 m. Although the growing season weather was generally warm and dry at both BP and DLP, a difference in precipitation is also possible because summer rainfall is predominantly due to localized thunderstorms and only BP precipitation was actually measured (Table 2). The higher soil moisture levels at DLP1 promote greater herbaceous biomass there (figure 4), which coupled with N inputs from inundation and sediment deposition (Adair et al. 2004) would lead to greater soil OM and nutrient pools.

Fertilization experiment

Although we found no consistent trend differentiating fertilized and unfertilized plot biomass at any site, we noted differences in the appearance of the two plots in some pairs that suggested herbivory was greater in the fertilized plot. In those plot-pairs where the fertilized plot held the smaller amount of biomass, the fertilized plot held, on average, 30% less biomass than the control plot (range 8 to 48%). In contrast, in plot-pairs where the fertilized plot held the most biomass, that biomass was, on average, 56%

greater than that of the control plot (range 20 to 179%). These values are consistent with the notion of localized or “spotty” differential herbivory that affected some plot-pairs but not others.

Two lines of evidence support the notion that herbivory was more intense in the fertilized plots at DLP. First, the assessment of total N in fresh green biomass collected in DLP and BP plot-pairs showed the N concentration was 27% higher in the fertilized plots. This provides direct evidence that the fertilization affected plants in the treated plots. Numerous studies show that ungulates and other herbivores will preferentially feed on plants containing higher levels of nitrogen ([Day and Detling 1990](#), [Steinauer and Collins 2001](#), [Denyer et al. 2007](#)). Deerlodge Park supports large numbers of both deer and elk. Secondly, our results are statistically improbable *if* fertilization did in fact increase plant growth. We found smaller biomass in the fertilized plot in 8 of the 15 plot-pairs. Assuming a positive fertilization effect on growth and that in the absence of differential herbivory biomass is measurably greater in at least 70% of plot-pairs, the probability of finding *smaller* biomass in the fertilized plot in 8 or more of the 15 pairs of plots is small ($P = 0.05$, calculated using the binomial distribution). That probability becomes much smaller ($P = 0.004$) if it is assumed the fertilization effect is stronger, i.e., that at least 8 out of 10 pairs of plots show the fertilizer effect in the absence of herbivory.

The dry growing season conditions may have led to moisture limiting herbaceous plant growth in addition to, or instead of, limitation by soil N. Fenn et al. ([2003](#)) argued that upland plant productivity in arid or semi-arid regions may be increased by nitrogen addition only in wet years because of primary controls from moisture limitations

Evidence for N-limitation

Laboratory analysis of a soil sample can provide information on the concentration of N immediately available to plants, but those concentrations do not provide an accurate picture of whether the plant-available N supply rate in the soil can meet the uptake demand of growing vegetation. We collected soil samples in the middle of the growing season (warm-desert sites) or at its end (cold-desert sites), when soil N could be depleted due to plant uptake. Such depletion is one possible explanation for the NO_3^- -N concentrations we observed (Table 3), which were all <10 ppm, the threshold commonly associated with low soil N in agricultural settings (citations). Total soil N includes the N bound in organic matter and potentially available to plants through decomposition (mineralization and nitrification processes). The total N values we observed, ranging from 0.01 to 0.31%, would also be considered low in an agricultural soil, where ??% is commonly stated as desirable for maximum production (citations).

Application of urea pellets increased soil PRS-N values on the floodplains of the Yampa and Green rivers. It also increased N content in floodplain foliage along both rivers. PRS- NO_3^- was the dominant contributor to PRS-N, and both PRS- NO_3^- and PRS-N were correlated with NO_3^- concentrations in soil, supporting the assumption that PRS-N was, in fact, indexing the plant-available N supply. Finally, in unmanipulated plots on the unregulated Yampa River, PRS-N level was positively related to aboveground productivity, as measured by herbaceous standing crop biomass at the end of the growing season. Taken together, these results strongly suggest that plants on the Yampa River floodplain are N-limited, at least in some growing seasons.

Evidence for N-limitation at BP is less clear. Our failure to find a relationship between PRS-N and biomass in the unmanipulated plots at BP1-*Gly* may reflect our inability to clearly differentiate current- and prior-year *Glycyrrhiza* stems. Alternatively, it may reflect the higher N availability at that site as reflected by mid-summer soil nitrate levels (Table 3). Our failure to link PRS-N and control plot biomass at BP1 or BP2 may reflect overwinter biomass losses coupled with the increased difficulty of differentiating 2012 and prior year's litter. Adair et al. (2004) found N mineralization and nitrification rates under young cottonwoods were higher in BP than DLP, and reported cottonwood leaf N concentration was also highest in BP. They suggested that the greater availability of soil N at BP might be due to organic matter accumulations or a more favorable environment for soil microbes, both potential effects of a moderated and stabilized flow regime.

Plant species differ in their N requirement and N-use efficiency, making extrapolation of the herbaceous productivity—PRS-N linkage found at DLP to the warm-desert sites at best suggestive. The BWR site most likely to be N-limited is BWR1b, where the mean PRS-N value was only 16. The picture at LVW is clouded by the fact that PRS-N there contained large contributions from ammonium, an N source that may or may not affect the plant in the same manner as nitrate. Whether the increased contribution from ammonium was related to the floods in LVW is unknown.

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Table 1. Attributes of rivers in the segments within which nitrogen nutrient dynamics in riparian soils were investigated.

River	ID code	Drainage area [†] (km ²)	Mean annual discharge (m ³ /s)	Flow regime alteration			
				Level	Source	Period of alteration	Form of alteration
Bill Williams	BWR	13823	~2.6	High	Alamo Dam	Since 1968	Eliminated most uncontrolled floods & stabilized base flow
Las Vegas Wash	LVW	3932	~8.5	High	Treatment-plant effluent	Incremental alteration since ~1930	Increased base flow, possibly increased flood peaks
Green	BP	50116	56	High	Flaming Gorge Dam	Since 1964	Reduced flood peaks & increased base flow
Yampa	DLP	20541	60	None	---	---	---

[†]Measured above gage used to monitor flow in this study.

Table 2. Periods during 2012 over which PRSTM Probes were deployed at the four study locations in the Colorado River Basin.

River	Group	Number of sites	Total number of plots	Probe deployment date	Probe recovery date	Exposure duration (days)	Total precipitation during exposure period (cm)
Yampa (DLP)	DLP1	2	6	9-10 April	31 July	112	4.4 ^a
	DLP2	3	9				
Green (BP)	BP1	2	6	11 April	1 August	112	≤ 1.4 ^b
	BP2	3	9				
	BP1- <i>Gly</i>	1	6				
Bill Williams (BWR)	BWR1	2	6	16 May	14 November	182	4.5 ^c
	BWR2	1	3				
Las Vegas Wash (LVW)	LVW	3	9	15 May	13 November	182	13.6 ^d

^aBased on mean of the sums of April-July monthly totals for three regional climate stations (051932, 052286, and 480484).

^bSum of April-July monthly totals measured on-site

^cBased on sum of May-November monthly totals for Parker Reservoir, AZ (station 046699)

^dBased on sum of May-November monthly totals for Las Vegas WSO Airport, NV (station 264436)

Table 3. Soil attributes for sites, grouped by landform, in three of the four locations where PRS-N was measured in the Colorado River Basin. Las Vegas Wash samples were not analyzed because of large erosion/sedimentation effects. Groups coded with a 1 are on floodplain landforms relatively high compared to those coded with a 2, but position is relative within rivers only. DLP and BP soils were sampled 31 July-1 August 2012, and BWR was sampled 14 November 2012. Groups identified with an asterisk are unpublished data for soil samples collected at nearby sites in 2002 (see Note) included for comparison. The number of individual soil samples (*n*) analyzed in each group is tabulated; the total is less than the number of plots examined because samples from selected plots were not analyzed due to budget constraints. Tabulated values are the mean with the standard error in parentheses. PRS-N values are for all plots within each group.

River	Group ID	Floodplain topographic position	<i>n</i>	Sand (%)	Clay (%)	pH	Electrical conductivity (dS/m)	Organic matter (%)	Total N (%)	NO ₃ -N (ppm)	PRS-N
Bill Williams	BWR1a	High	3	60 (4)	23 (1)	7.8 (0.12)	1.3 (0.26)	0.9 (0.20)	0.01 (0.005)	6.6 (3.24)	187 (49)
	BWR1b	High	2	62 (2)	26 (2)	7.7 (0.10)	2.4 (1.15)	0.7 (0.10)	0.02 (0.004)	1.3 (0.80)	16 (11)
	BWR2	Low	2	56 (12)	30 (6)	7.7 (0.05)	1.8 (0.15)	1.8 (1.00)	0.06 (0.01)	6.6 (1.95)	46 (6)
Las Vegas Wash		Low									17 (9.8)
Yampa	DLP1	High	5	18 (3.1)	47 (4.1)	7.5 (0.03)	0.6 (0.07)	3.0 (0.5)	0.13 (0.007)	2.1 (0.20)	36 (11.9)
	DLP1*	High	2	27	34	7.3	3.2	3.3	0.16	2.1	

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	DLP2	Low	6	21 (7.2)	39 (3.4)	7.7 (0.02)	0.7 (0.07)	2.2 (0.34)	0.09 (0.02)	0.4 (0.06)	8 (1.7)
	DLP2*	Low	2	35	16	7.7	1.6	2.2	0.10	0.8	
Green	BP1	High	5	40 (2.8)	33 (3.4)	7.9 (0.05)	0.6 (0.07)	1.6 (0.23)	0.06 (0.01)	0.7 (0.09)	15 (3.8)
	BP1*	High	1	22	30	7.5	5.0	1.7	0.11	1.8	
	BP1- <i>Gly</i>	High	5	24 (2.3)	47 (1.3)	7.7 (0.08)	0.5 (0.02)	5.1 (0.62)	0.31 (0.03)	2.3 (0.26)	25 (5.4)
	BP2	Low	6	47 (5.9)	27 (1.0)	7.8 (0.02)	0.4 (0.04)	1.1 (0.15)	0.05 (0.01)	0.9 (0.28)	23 (10.1)
	BP2*	Low	1	62	8	7.9	4.0	1.1	0.07	0.8	

Note: The 2002 soil samples are composites collected 14 June 2002 at DLP and 14 August 2002 at BP.

Table 4. Efficacy of urea fertilization as determined by 1-sided paired *t*-tests comparing PRS-N values for plot-pairs grouped by landform at DLP on the unregulated Yampa River and at BP on the highly-regulated Green River. We hypothesized greater N supply in the fertilized plot of each pair, and thus tested whether the difference between treatment and control plot PRS-N value in each pair > 0 . The mean ratio (\pm SE) of the PRS-N values for the plot-pairs (fertilized/control) is also shown.

Location	Site/Group	<i>t</i>	<i>df</i>	<i>P</i>	Mean ratio
DLP	DLP1	-3.97	5	0.005	7.65 \pm 1.94
	DLP2	-2.68	8	0.014	5.44 \pm 1.65
BP	BP1	-2.25	8	0.027	10.76 \pm 4.56
	BP2	-2.46	5	0.028	4.02 \pm 1.24
	BP1- <i>Gly</i>	-5.50	5	0.001	2.12 \pm 0.22

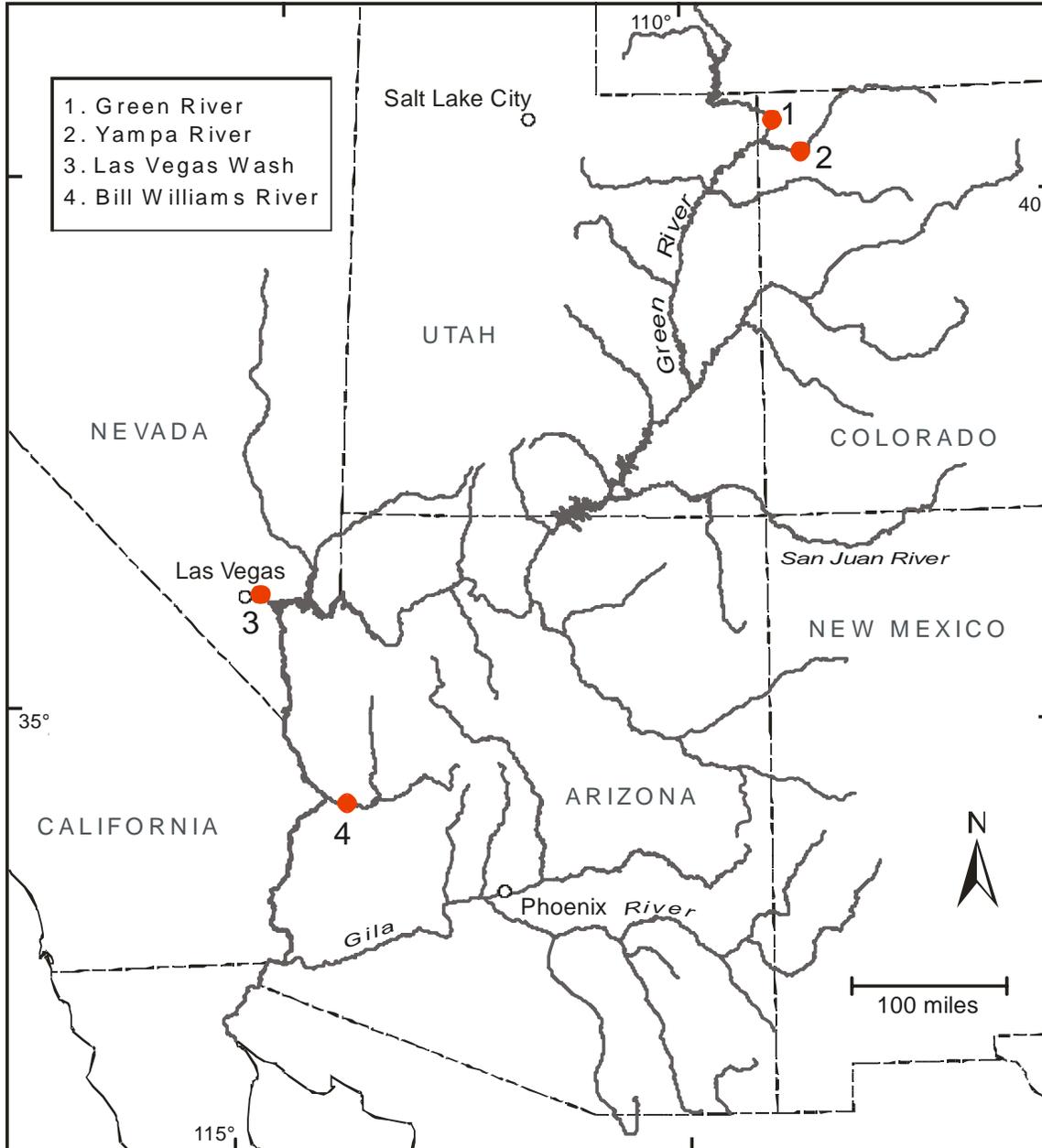


Figure 1. Locations of the four study segments on the Green (BP), Yampa (DLP), and Bill Williams (BWR) rivers and Las Vegas Wash.

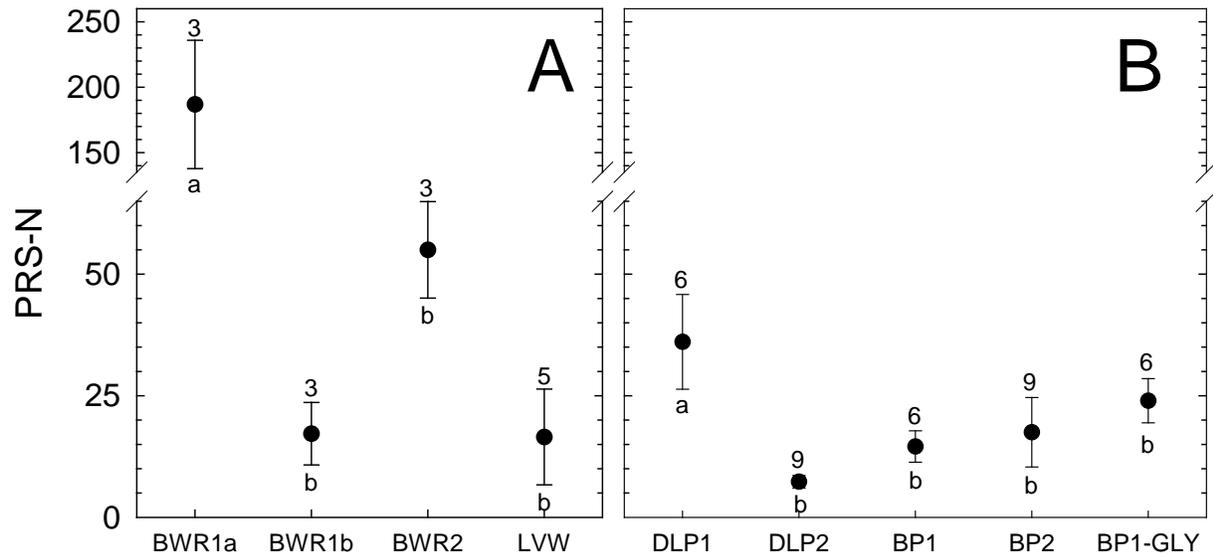


Figure 2. Mean PRS-N values (± 1 SE) for (A) warm-desert riparian sites along the Bill Williams River (BWR) and Las Vegas Wash (LVW) and (B) cold-desert sites along the Yampa (DLP) and Green (BP) rivers. Note the scale change to accommodate Site BWR1a. Sites are pooled by landform where appropriate; within a location, groups coded with a 1 are in higher floodplain positions than groups coded with a 2. All data are from unmanipulated (control) plots. The number of plots is indicated above the standard error bar. Within each panel, means sharing the same letter below the error bar are not significantly different.

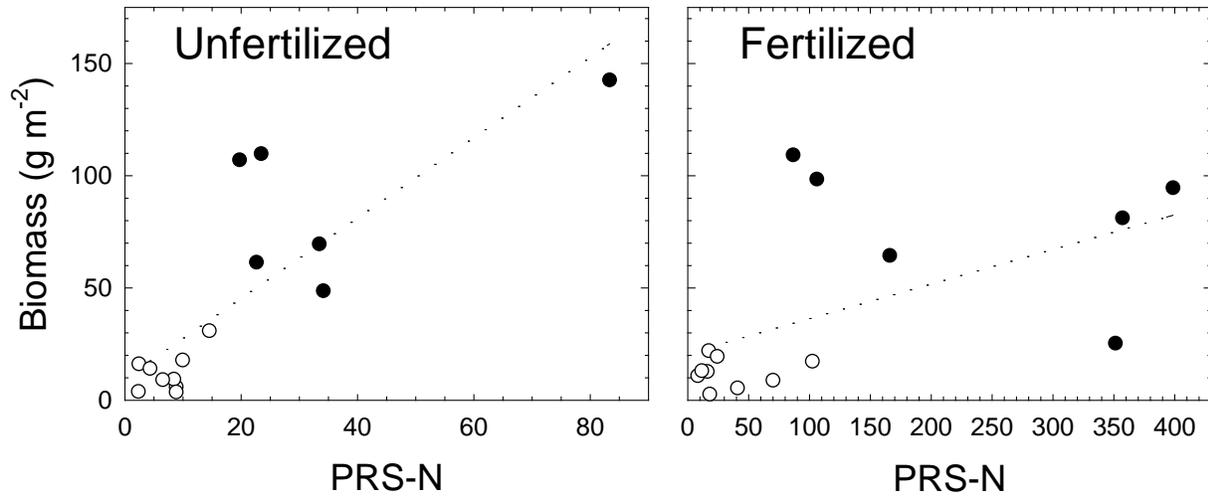


Figure 3. Herbaceous biomass collected at the end of the growing season from each of the DLP unfertilized (control) plots (left panel) and fertilized plots (right panel) plotted against the PRS-N value for that plot. Filled circles are plots in the relatively high DLP1 area and open circles are plots in the lower, DLP2 area. The dashed line is the least-squares linear regression (unfertilized: $r^2 = 0.67$, $P < 0.001$; fertilized: $r^2 = 0.30$, $P = 0.034$).

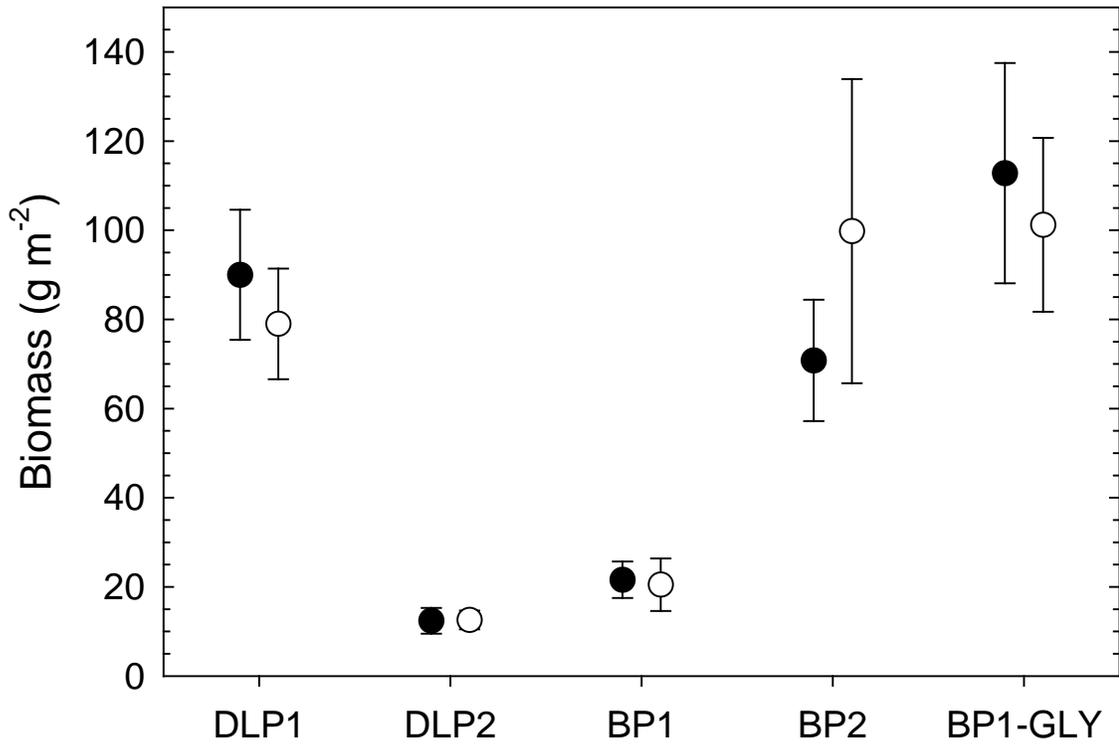


Figure 4. Mean aboveground standing crop biomass (± 1 SE) of herbaceous plants at the end of the 2012 growing season in paired control (filled circles) and fertilized (open circles) plots at sites on the Yampa (DLP) and Green river (BP) floodplains

Data Sets that support the final report

Share Drive folder name and path where data are stored:

H:EnvResShare/8668220/X0015_Nutrient data

Point of Contact name, email and phone:

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Short description of the data:

Nutrient data from sample sites.

Keywords:

Nitrogen, soil analysis, litter biomass

Approximate total size of all files: 94 KB

