

Carbon and Water Relations of *Salix monticola* in Response to Winter Browsing and Changes in Surface Water Hydrology: An Isotopic Study Using $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

By

Karrin P. Alstad¹
Jeff M. Welker²
Stephen A. Williams²
and
Milton J. Trlica³

Abstract. To ascertain whether browsing or hydrologic conditions influence the physiological performance of willow (*Salix* spp.) and whether willows and graminoids (*Carex*) use and possibly compete for similar water resources, we quantified the *in situ* seasonal patterns of plant water and carbon relations over three growing seasons. Our studies were designed to address the physiological factors which may be responsible for poor woody plant regeneration in montane riparian habitats of Rocky Mountain National Park, Colorado. As these systems act to insure the delivery of fresh water to downstream users, the maintenance of their integrity is critical. We quantified plant water potentials, instantaneous rates of carbon fixation, leaf carbon isotope discrimination (Δ), leaf nitrogen content, and water sources using stable isotopes of water ($\delta^{18}\text{O}$). The carbon and water relations of willow were significantly affected by winter grazing by elk and in some cases, by landscape position with regards to proximity to active streams. Winter grazing of willow by elk significantly increased summer plant water potentials and integrative measures of gas exchange (Δ), though grazing did not consistently affect instantaneous rates of photosynthesis, leaf nitrogen nor the sources of water used by willow. No effect of experimental manipulations of surface water conditions on willow physiology was observed, likely due to the mesic nature of our study period. Using a two-member linear mixing model from $\delta^{18}\text{O}$ values, we calculated that willow appears to rely on streams for approximately 80% of its water. In contrast, sedges derive almost 50% of water from rainfall, indicating divergent water source use by these two life forms.

Based on these findings, winter grazing by elk improved willow water balance by possibly altering the shoot to root ratio which in turn leads to higher water potentials and higher degrees of season-long gas exchange while experimental damming had in general no effect on the physiological performance of willow plants. In addition, as the water sources of willow and sedge were significantly different, competition for water may not influence the growth, development and regeneration of willow. Thus, under the conditions of our study, herbivory had a positive effect on the physiological performance of willow, but it is still unclear whether these changes in physiology transcend into improved willow regeneration and survivorship. However, under drier environmental conditions such as lower snow packs and lower stream flows, grazing resistance of willow and ecosystem regeneration may be greatly hindered as willow's reliance on stream water indicates its vulnerability to changes in surface water and hydrological conditions.

Keywords: Plant-animal interactions, riparian ecosystems, Rocky Mountain National Park, stable isotopes, ungulates.

Reprinted with kind permission from Springer-Verlag. Alstad, K. P., J. M. Welker, S. A. Williams, and M. J. Trlica. 1999. Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: An isotopic study using $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. *Oecologia* 120:375–385.

¹Department of Forestry, Northern Arizona University, Flagstaff, Arizona 86011

²Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523

³Department of Rangeland Ecosystem Science, Colorado State University, Fort Collins, Colorado 80523

Introduction

The carbon and water relations of native plants in riparian ecosystems are currently receiving attention because their physiology may influence community and ecosystem sustainability (Dawson and Ehleringer 1991; Busch and Smith 1995; Svejcar and Trent 1995; Dawson and Pate 1996; Kolb et al. 1997; Pimentel et al. 1997; Gleick 1998). Adequate regeneration of these ecosystems is essential to maintaining acceptable levels of biodiversity and the structural and functional aspects of habitats that deliver ecosystem services such as clean water (Naiman et al. 1995, 1998; Gleick 1998). There are, however, a host of woody dominated systems, which apparently are not regenerating adequately (Gordon et al. 1989; Singer et al. 1994, 1997; Kolb et al. 1997). The extent to which herbivores, changes in surface water conditions due to beaver (Naiman et al. 1988, 1994), and competition for water with herbaceous neighbors may all be influencing the physiology, growth, reproduction, and regeneration of woody species in riparian systems is, however, unclear.

Herbivory can influence growth and the physiological performance of plants (Coughenour et al. 1985; Toft et al. 1987; Welker and Menke 1990; Welker and Briske 1992; Busso and Richards 1995; Fahnestock and Detling 1999). For instance, herbivory may alter carbon and nitrogen allocation (Welker et al. 1985, 1987), rates of carbon assimilation (Caldwell et al. 1981; Detling and Painter 1983; Wallace et al. 1984) as well as plant water balance (Welker and Menke 1990; Day and Detling 1994). Whether herbivory and browsing have a positive or negative effect on plants may depend in part on environmental condition (Georgiadis et al. 1989) as changes in root to shoot ratio following browsing may be beneficial to the water balance of plants (Welker and Menke 1990) while the removal of meristems may reduce their future growth potential (Briske 1986).

Beaver (*Castor canadensis*) clearly impact the distribution of surface water across riparian ecosystems and greatly influence the biogeochemical cycles of these habitats (Naiman et al. 1988, 1994). Beaver impact woody species in these systems in both direct and indirect manners; directly by harvesting mature individuals for dam construction and indirectly as dams act to slow river or stream flows causing ponding and the dispersal of water across the floodplain (Naiman et al. 1994, 1995). This flooding may be an important component of willow (*Salix* spp.) plant survival (Singer et al. 1994) by maintaining

high water potentials, which may enhance carbon gain improving the resistance of these plants to periodic browsing by ungulates (Svejcar and Trent 1995). Consequently, in regions where beaver have been trapped-out and harvested, willow plant water and carbon relations may be hindered, grazing resistance may be lower, and willow plant survivorship and ecosystem regeneration possibly threatened.

Herbaceous neighbors may compete with woody plants for belowground resources (Gordon et al. 1989; Callaway and Walker 1997) extracting water or nutrients at rates or to degrees which hinder woody plant resource acquisition, growth and possibly ecosystem regeneration (Gordon et al. 1989; Welker et al. 1991). These measures of competitive interactions between divergent life forms in montane riparian habitats have seldom, however, been demonstrated using stable isotope techniques (Dawson and Ehleringer 1991; Dawson 1993) which provide direct evidence for common use of groundwater as opposed to rainfall (Busch and Smith 1995; Dawson and Pate 1996; Dodd et al. 1998). One would anticipate that both herbaceous and woody plants in riparian ecosystems would have access to and utilize common water resources as grasses often have deep root systems which overlap with shrubs (Dodd et al. 1998). If these life forms utilize common resources, it is possible that herbaceous neighbors may extract resources that are necessary for woody plant growth and development which could hinder juvenile or mature woody plant regeneration (Gordon et al. 1989; Callaway and Walker 1997).

To study how browsing and surface water conditions affect willow physiology, and whether willow and herbaceous vegetation use similar water sources, we have quantified seasonal patterns of plant water and carbon relations *in situ* over 3 years where elk were present and excluded, and where surface water was artificially dammed and left undisturbed. We have used a host of approaches, at a multitude of temporal scales, from instantaneous rates of carbon fixation to integrative measures of leaf gas exchange ($^{13}\text{C}/^{12}\text{C}$ ratios) plus an examination of water sources using stable isotopes of water ($\delta^{18}\text{O}$), for both woody and herbaceous species (Ehleringer 1991; Ehleringer and Dawson 1992; Welker et al. 1995; Dodd et al. 1998) because we recognize that field measurements of instantaneous physiological performance can be limited in scope, especially where sampling occurs over several days, and that accurate interpretation of plant responses often requires a host of parameters (Caldwell et al. 1981; Chapin et al. 1987; Welker et al. 1997). We had three primary objectives: (1) to determine whether the carbon and water relations

of willow are influenced by elk browsing and modifications of surface water hydrology; (2) to quantify whether the carbon and water relations of riparian vegetation is influenced by landscape position (adjacent to or distant from active stream channels); and (3) to quantify and compare the water sources of willow and herbaceous neighbors (*Carex* spp.) and their carbon relations as indicators of potential competition for similar water sources.

Materials and Methods

Study Sites

Our study sites were in riparian ecosystems on the northeast side of Rocky Mountain National Park. Two willow-dominated communities in the winter range of a migratory elk (*Cervus elaphus*) herd were selected within Moraine Park in the Big Thompson River watershed (elevation 2,481 m) and in Horseshoe Park of the Fall River watershed (elevation 2,598 m). The two watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters (Baron 1992). Willow species, primarily *Salix monticola*, *Salix geeyeriana*, and *Salix planifolia*, are dominant in both watersheds with *Salix monticola* being the primary target species used in our study. The understory of these riparian areas was predominantly *Potentilla* shrubs and graminoids dominated by sedge species which form a continuous cover within the willow plant matrix. The 30-year average temperature in the Estes Valley ranges from 9° to 17°C during the 5-month growing season of May through September. The average total precipitation during the growing season averages 37 cm with >70% occurring in May and June (Colorado Climate Center 1995, 1996). Average peak snowpack level is 51 cm (snow water equivalent), and occurs in mid-April while peak stream flow typically occurs in early to mid-June (USDA 1995 and 1996).

Experimental Treatments

The study was designed as a randomized complete block experiment with a factorial arrangement of treatments, which included four replications (blocks) across both watersheds with two levels of grazing, grazed and ungrazed. The ungrazed treatments were established within four exclosures (46 m x 30 m) that were erected within each watershed between August and November of 1994 (eight exclosures total). An area surrounding

each exclosure (approximately 100 m radius) was used as the corresponding grazed area used by elk during winter. We attempted to manipulate increases in the water table of several sites, as might occur if beaver dams were present in the area, by installing small check dams (1 cm thick sheet metal) in ephemeral stream channels in two of the study sites in Moraine Park and two sites in Horseshoe Park. This affected the surface water conditions for both an ungrazed and adjacent grazed area. Treatments with water additions will be referred to as short-watered willow sites. Sites with no water table manipulations will be referred to as short-control willow sites.

Field Measurements of Carbon and Water Relations

Salix monticola shrubs of medium height (0.75 to 2.0 m) were selected in close proximity to streams ("streamside") and in areas distant from streams ("upland") at least 10 m in a horizontal direction from streams and usually <0.5 m higher than streamside plants). Within 2 m of target willow plants, portions of sedge plants (10 cm diameter area) were excavated to 5 cm, which allowed us to retrieve nonphotosynthetic crown material for water extraction and photosynthetically active leaves for nutrient and $\delta^{13}\text{C}$ analysis (Ehleringer and Cooper 1988; Ehleringer 1991). Sedge material was collected three times in 1997, mid-June, mid-August and mid-September in both streamside and upland locations.

Willow physiological measures were carried out during 2-week periods each month throughout the summer from full leaf expansion to leaf senescence beginning in June and continuing through September of 1995 and 1996. In 1997, willow physiological measures were taken less frequently. In 1995 and 1996, midday willow leaf gas exchange measures were made between 1000 and 1300 hours, once during each 2-week period. A LICOR 6200 portable photosynthesis system (LI-COR, Inc., Lincoln, Nebraska) equipped with 0.25-L leaf chamber was used to determine instantaneous photosynthetic rates while recording photosynthetically active radiation (PAR). Air temperatures were also recorded at this time from the leaf chamber thermocouple when the fan was running and the chamber was open before gas exchange measurements. Area-specific photosynthesis results were calculated using the single leaf surface enclosed in the chamber. Willow leaves used for photosynthetic measurements were dried, ground, and analyzed for nitrogen content and carbon isotope ratios ($\delta^{13}\text{C}$) (Ehleringer 1991).

Willow total water potentials were measured on the same day as photosynthesis measures between 1100–1400 hr using the pressure chamber technique (Welker and Menke 1990). Representative leaders from the upper canopy of target shrubs were severed, immediately placed in the pressure chamber and total water potential was determined. The stems were then stripped of leaves, sealed in glass vials, placed on ice, and transported back to the lab and stored frozen until the xylem water was extracted and analyzed for $\delta^{18}\text{O}$ (Ehleringer and Osmond 1989; Dawson and Ehleringer 1991).

Monthly water samples for source water evaluation ($\delta^{18}\text{O}$) were collected from snow, groundwater wells which had a maximum depth of 2 m, stream surface water, and rain (Ehleringer and Dawson 1992; Dodd et al. 1998). Snow was collected in the two main watersheds in April by coring using a 5 cm x 30 cm tube. Each core was homogenized in a zip lock bag and a subsample placed into a 250 ml Nalgene bottle (acid washed and dried). The bottles were capped, sealed with Parafilm, placed into a cooler, transported to the laboratory and kept frozen until isotopic analysis for $\delta^{18}\text{O}$. Five representative cores were collected between our grazing exclosures. Stream water was collected at midday by placing a 250 ml Nalgene bottle just below the water surface in mid-stream, capping the bottle with little headspace, and sealing the cap with Parafilm. The sample was then placed in a cooler which was then transported back to the laboratory and the water samples frozen until $\delta^{18}\text{O}$ analysis. Well water was collected by inserting a Teflon tube down to the water level, and with the use of a hand pump, water was collected into a 250 ml Nalgene bottle, capped, sealed and transported in a similar manner as were the stream water and snow samples. Rain was collected in plastic gauges that contained oil to prevent evaporative enrichment (Dodd et al. 1998). Water samples were sealed, placed on ice, transported from the field and stored frozen until analysis. Snow-pack data was derived from the SNOTEL data center for the Willow Park collection station approximately 10 km upstream of the Horseshoe Park study site.

Isotopic ($\delta^{13}\text{C}$) and Nitrogen Analyses

For the analysis of leaf tissue $\delta^{13}\text{C}$ abundance, leaves of willow and sedge were dried at 60°C for 72 hrs, and then ground in a ball mill to a fine powder and subsamples (<0.01 g) were combusted at 800°C in a Carlo-Erba NA 1500 Series 2 Carbon and Nitrogen analyzer attached to a VG-Optima® mass spectrometer. The mass spectrometer was initially calibrated against the

NBS 22 primary standard while vacuum pump oil with a $\delta^{13}\text{C}$ value of -27.00 + - 0.20 relative to Pee Dee Belemnite (PDB) used as a secondary standard in each batch of samples. The sample $\delta^{13}\text{C}$ values are expressed relative to the standard for carbon, PDB (Craig 1957) using the equation:

$$\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$$

where $\delta^{13}\text{C}$ is the carbon isotope ratio of the sample in parts per mil (‰), R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ratios of sample and standards, respectively. The precision of each isotope measurement is 0.03‰. The $\delta^{13}\text{C}$ values were then converted to the discrimination (Δ) value where:

$$\Delta = \delta^{13}\text{C}_{\text{sample}} - \delta^{13}\text{C}_{\text{standard}} / \delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{standard}}$$

(O'Leary 1981; Farquhar et al. 1982). The $\delta^{13}\text{C}$ of the air was assumed to be -8‰ (Farquhar et al. 1989). The Δ values are integrative indicators of intercellular CO_2 concentration, which is affected by the balance between the leaf photosynthetic capacity and stomatal conductance (Farquhar et al. 1982). Willow leaves used for instantaneous gas-exchange measurements were also subsampled and used for analysis of foliar nitrogen concentration using a LECO CHN analyzer (LECO 1993). Since leaf photosynthate comprises more than 75% of total leaf N, these concentrations give an estimate of leaf Ribulose activity and complement information for analysis of photosynthesis activity. Both total nitrogen concentration and instantaneous gas-exchange measures were related to the carbon discrimination values to determine whether increases in leaf carbon isotope discrimination values were caused by increased carbon assimilation rates or increased stomatal conductance (Evans et al. 1986).

Plant Water Extraction and $\delta^{18}\text{O}$ Analysis

We extracted xylem water from plant stem tissue for willow and from nonphotosynthetic crown tissue of sedge (Dodd et al. 1998) using a vacuum distillation extraction line (Ehleringer and Osmond 1989). Plant tissue was placed into a glass vial that was subsequently evacuated to 10^{-3} mbar. The vial was then heated by immersion in boiling water for 3 hours to evaporate the free water. The evaporated water was collected in a cold finger by freezing with an ethanol-dry ice slurry. We then took 0.2 ml subsamples of the extracted water and transferred them to 1.0 ml glass vials, thoroughly

aspirated the vials with CO₂ in a glove bag and equilibrated each batch for 10 hours at 40°C. The isotopic composition of the CO₂ in the headspace was measured using a multiprep sampler connected to a dual inlet VG-Optima® mass spectrometer (Epstein and Mayeda 1953; Ehleringer and Osmond 1989).

The sample δ¹⁸O values are expressed relative to the standard for oxygen, V-SMOW (Vienna Standard Mean Ocean Water) using the equation:

$$\delta^{18}\text{O} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$$

where δ¹⁸O is the oxygen isotope ratio of the sample in parts per mil (‰), R_{sample} and R_{standard} are the ¹⁸O/¹⁶O ratios of sample and standards, respectively. The precision of each isotope measurement is 0.2%.

The usual primary standard for oxygen is V-SMOW, although the δ values of the samples and three secondary standards were calculated using a linear calibration of the mass spectrometer against three primary standards of known δ values: V-SMOW, GISP, and SLAP (Gat 1980). The standard V-SMOW replaced the original primary oxygen standard SMOW, which was subject to characterization problems, and which has since been exhausted (Ehleringer and Dawson 1992). The three secondary standards we used were deionized tap water (DI); “cooked” deionized water (DI boiled for 12 hours); and snowmelt collected from Cameron Pass, Colorado, and all three were used in each batch of samples. We calculated the δ¹⁸O abundance values of the water samples relative to V-SMOW by adjusting for any shift in the secondary standard occurring in separate batches, and applying the original linear calibration equation, as follows:

$$\text{actual } \delta^{18}\text{O} = 0.98 \times \text{observed } \delta^{18}\text{O} - 6.211, r^2 = 0.98.$$

The use of the calibration equation takes account of the fractionation coefficient of the H₂O-CO₂ equilibrium, and the contribution of O from the tank CO₂ used to aspirate the samples. In any case, the latter factor can be considered negligible, based on a 125:1 ratio of O in H₂O vs. CO₂ in the vials.

Comparisons of the δ¹⁸O values of the source waters against the δ¹⁸O values of the willow and sedge xylem water were made to evaluate the water sources used by riparian vegetation (Dawson and Pate 1996; Feild and Dawson 1998) and a simple two-end-member linear mixing model was used to calculate the proportion of rain water and subsequently groundwater in willow and sedge stem tissue (Feild and Dawson 1998). The two-end-members were defined by the average of stream

and groundwater (-16.1%) and the average in summer rainfall (-7.0%). We calculated the rainwater proportion (P_r) in our plants by the ratio of the distances between groundwater δ¹⁸O (δ¹⁸O_{gw}) and rain δ¹⁸O (δ¹⁸O_r) and rainwater δ¹⁸O (δ¹⁸O_r) and plant xylem water δ¹⁸O (δ¹⁸O_p) (willow and sedge) (adapted from Feild and Dawson 1998), as:

$$P_r = (\delta^{18}\text{O}_{\text{gw}} - \delta^{18}\text{O}_p) / (\delta^{18}\text{O}_{\text{gw}} - \delta^{18}\text{O}_r).$$

We were assured that the xylem water we extracted was unfractionated source water by measuring the δ¹⁸O values of willow stem bases, current and previous years growth, which we found to be similar (Singer et al. 1997, 1998).

Statistical Analysis

Leaf CO₂ assimilation rates, N concentrations, stem water potential, leaf carbon isotope discrimination, and stem water δ¹⁸O values were analyzed using a split-plot factorial design where watershed was considered a random effect (Ott 1993; SAS Institute Inc. 1995). Watersheds were not significantly different ($P < 0.05$), therefore the data values from both Moraine Park and Horseshoe Park were pooled in the analysis to determine the effects of browsing, surface water hydrology, and proximity to streams. Analysis of variance (mixed procedure) (SAS Institute Inc. 1995) was used to test for significance at $P < 0.05$. Under our set of circumstances, we chose to use ANOVA as opposed to MANOVA as our response variables were limited and the scale of the response variables was appreciably different as in the case of instantaneous rates of photosynthesis compared to leaf carbon isotope discrimination (Potvin et al. 1990). A MANOVA may have improved the power of our statistical test, but the ANOVA results represent the most conservative findings and thus those are presented here. For source-water utilization differences between willow and sedge, we used a student's *t*-test ($P < 0.05$).

Results

Precipitation

Snowfall and Runoff

Over the course of our 3-year study, peak snowpack levels were above the long-term averages for Rocky Mountain National Park (Fig. 1) though their

accumulation and dissipation patterns were different. Snowpack peaked in mid- to late-May in 1995, which was almost 30 days later than the long-term average (Fig. 1). In 1996, peak snowpack occurred close to that of the long-term average date in early May, which was similar to 1997, though the snow water equivalent at peak snowpack in 1997 was 30% greater than the long-term average. These snowpack characteristics transcended into some year-to-year variation in peak river levels; peak river levels in 1997 reaching 1 m in early June, 0.7 m in mid-June in 1996 and peak river levels of >1 m in late June in 1995 (Singer et al. 1997, 1998). In all years, once peak river depths had been reached, river levels gradually declined over the summer reaching their lowest levels in September, though precipitation events of 1 cm did slightly increase river

levels for up to 1 week by up to 0.1 m (Singer et al. 1998).

Summer Rainfall

Summer precipitation is sporadic in the Rocky Mountain region. In general, summer rainfall begins in May with individual events being usually less than 1 cm though large showers can occur (Niwt Ridge LTER database; Alstad 1998). During our 3-year study period, the average daily precipitation was slightly higher in 1995, averaging 0.3 cm or approximately 47 cm for the summer period (150 days), while in 1996 summer rainfall was lower averaging 0.2 cm per day (30.5 cm total) (Fig. 2). Summer rainfall in 1996 was substantially less

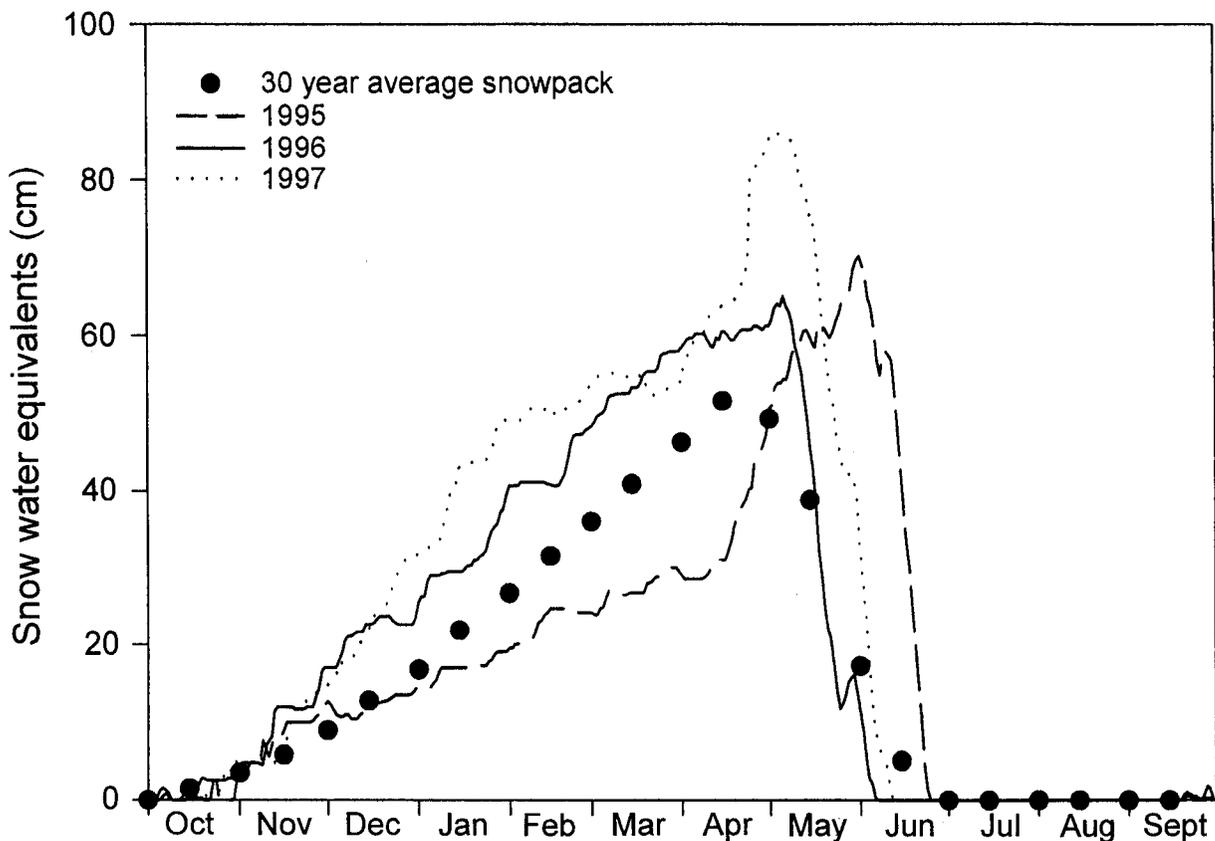


Fig. 1. Snowpack above Willow Park, Rocky Mountain National Park. Long-term (1961–1990) average versus 1995, 1996, 1997 water years. (Data from USDA Snow Survey Office Lakewood, Colorado, 1995, 1996, 1997.)

than in 1995 and 1997, especially in the months of June, July and August.

Total Plant Water Potentials

Stem water potentials of willow were significantly higher ($P < 0.01$) in 1995 as compared to 1996, averaging -0.6 MPa ($n = 55$) in 1995 and -0.9 MPa ($n = 68$) in 1996. In 1995, stem water potentials of willow decreased significantly from June (-0.54 MPa) to early September (-1.1 MPa) (Fig. 3a). There were no significant differences in plant water potentials between ungrazed and grazed plants, between plants in the short-watered willow sites and short-control willow sites, or between plants from different landscape positions in 1995. The total water potentials of willow plants decreased significantly ($P < 0.05$) over the course of the 1996 growing season, as well, (Fig. 3b) with grazed willow plants having higher water potentials than ungrazed plants ($P < 0.05$). Consequently, willow water potential exhibits a significant ($P < 0.02$) 2-way interaction where during the drier year; herbivory resulted in significant increases in plant water potentials. Water table manipulation (short-watered treatment) did not affect

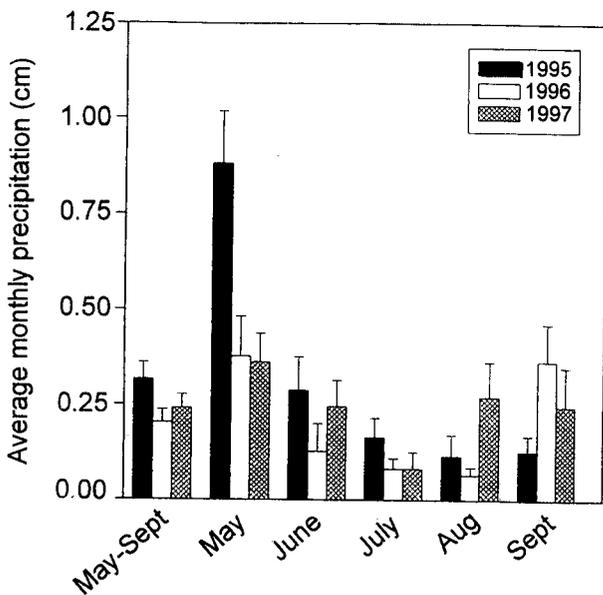


Fig. 2. Average monthly precipitation (cm) for the 1995, 1996, and 1997 growing seasons, Willow Park Climate Station, Rocky Mountain National Park. (Data from the USDA Snow Survey Office Lakewood, Colorado, 1995, 1996, 1997.)

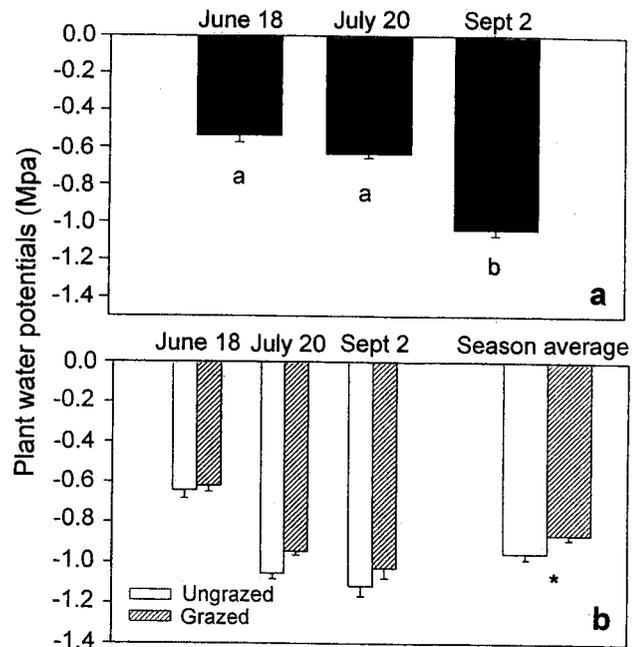


Fig. 3. *Salix monticola* plant water potentials for three sampling dates in 1995 (a) and 1996 (b) growing season and the yearly average water potentials for the grazed versus ungrazed (control) plants in 1996 (mean and S.E.). Different letters indicate significant ($P < 0.05$) differences between sampling dates. Significant differences between grazed and ungrazed (control) plants are noted with a * at $P < 0.05$.

willow water potentials in either year, nor were there significant differences in the total water potentials between plants that were streamside as opposed to those in upland positions.

Instantaneous Photosynthetic Rates

Instantaneous CO_2 assimilation rates of willow plants were not significantly ($P > 0.05$) different between 1995 and 1996, averaging $12.3\text{-}\mu\text{mol m}^{-2}\text{s}^{-1}$. The rates of leaf CO_2 assimilation did not differ significantly between the June, July and September, though higher rates of assimilation in grazed willow plants were observed but only in July ($P < 0.05$) (Fig. 4a). Higher rates of carbon assimilation were also observed in plants that were streamside, though only where check dams had been installed and this only occurred in July ($P < 0.05$) (Fig. 4b).

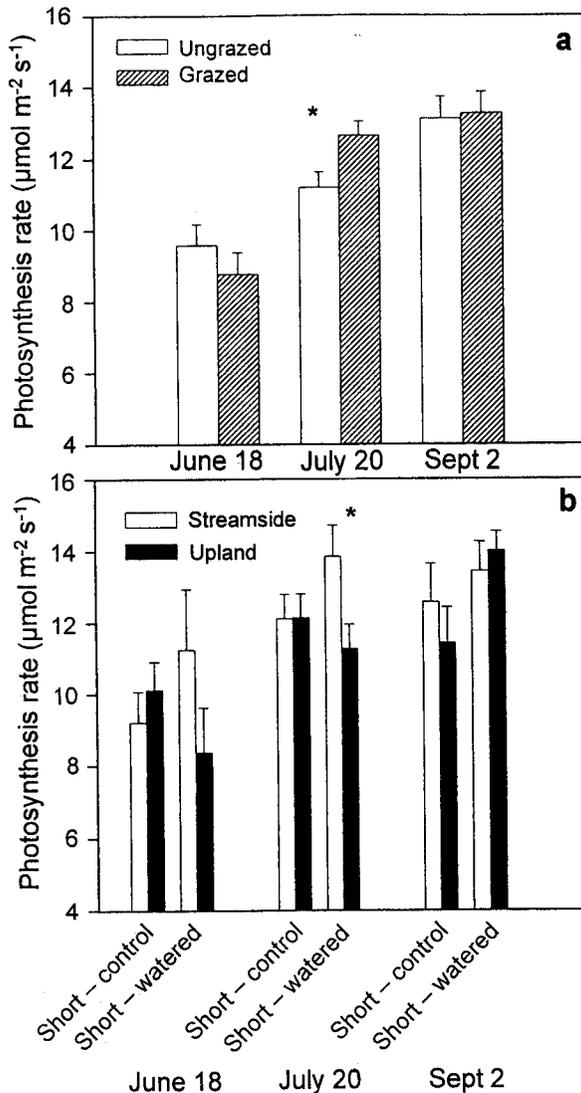


Fig. 4. *Salix monticola* photosynthetic rates for 1995 and 1996 growing seasons combined for grazed versus ungrazed (control) plants (a) and for plants that were streamside as opposed to located in upland positions where streams were either undammed or artificially dammed (mean and S.E.). An * indicates significant differences at $P < 0.05$ for grazed or ungrazed plants or plants that were located adjacent to streams or in upland positions.

Leaf Nitrogen

Leaf nitrogen content of willow plants decreased significantly ($P < 0.05$) between June and September (Fig. 5) while no significant differences between years were found. Leaf nitrogen contents were initially 3.2%, remained near this level through July, and decreased to 2.1% in September before leaf senescence. Grazed willow plants exhibited significantly ($P < 0.05$) higher leaf N contents in June compared to ungrazed plants though these differences were diminished by September. Leaf nitrogen content was not affected by damming nor were the leaf N contents different between streamside plants and those in upland locations.

Leaf Carbon Isotope Discrimination

Overall, the leaf carbon isotope discrimination (LCID) was significantly ($P > 0.001$) higher for willow

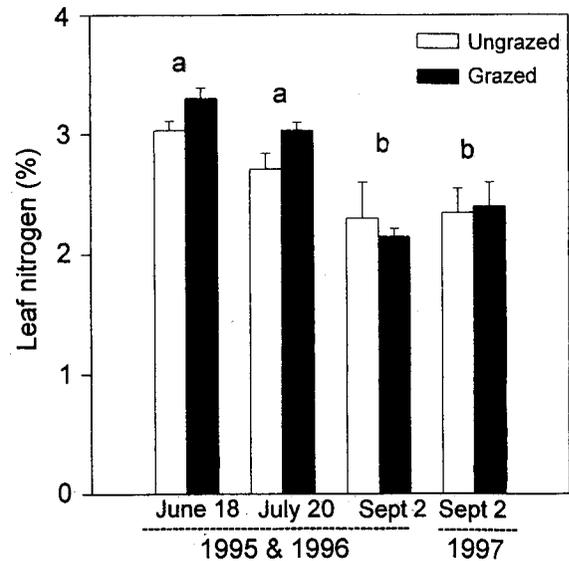


Fig. 5. Leaf nitrogen content (%) of ungrazed (control) and grazed plants for three sampling dates in 1995 and 1996 combined and for September in 1997 (means and S.E.). Different letters indicate significant differences, $P < 0.05$, between sample dates.

(20.5%) as opposed to that for the graminoid sedge that averaged 19.6% (data not shown). These differences were about 1%, representing a difference of approximately 30-ppm internal CO_2 concentrations (Donovan and Ehleringer 1994), which could be the result of species-specific differences in gas exchange, differences in leaf temperatures (Ehleringer et al. 1992) or possible differences in CO_2 sources (atmospheric vs. soil respired).

The LCID of willow plants harvested at the end of the growing season were found to be significantly ($P < 0.05$) different between years for ungrazed plants (Fig. 6a). Carbon isotope discrimination was significantly ($P < 0.05$) lower in 1996 compared to 1995 and 1997, by up to 1%. Grazing, too, significantly ($P < 0.003$) affected the LCID of willow, with grazed plants having higher overall discrimination values compared to plants that were ungrazed in all years (Fig. 6b). Proximity to stream channel also affected the LCID of willow plants whereby plants adjacent to active stream channels had higher Δ values than plants away from stream channels, though this response was only significant ($P < 0.05$) in year two (Fig. 6c). The Δ values of sedge were unaffected by proximity to stream channels.

$\delta^{18}\text{O}$ of Precipitation, Stream Water, and Plant Xylem Water

The average $\delta^{18}\text{O}$ values of the snow collected in late May in the riparian zone was -16.4‰, while the $\delta^{18}\text{O}$ values of summer rain collected near the study sites averaged almost -8‰ (Fig. 7a). Over the course of the summer, stream water was depleted in $\delta^{18}\text{O}$ compared to summer rain, which became progressively enriched between May and October (Fig. 7b). Both stream water and groundwater collected from wells within the experimental sites, had $\delta^{18}\text{O}$ values almost identical to that of snow, averaging -16.1‰. The $\delta^{18}\text{O}$ values of snow, stream and groundwater (well water) were very similar and were not significantly different, though on average willow $\delta^{18}\text{O}$ values were enriched compared to stream water while sedge xylem water $\delta^{18}\text{O}$ values were significantly ($P < 0.001$) enriched compared to stream water. Willow and sedge $\delta^{18}\text{O}$ values were significantly different ($P < 0.001$; Fig. 7a).

The $\delta^{18}\text{O}$ values of willow xylem water was not significantly different between plants that were streamside or in upland positions. In addition, the $\delta^{18}\text{O}$ values of xylem water in willow plants that were grazed by elk were not significantly different than those that were not grazed (Table 1) nor were there significant

changes in the $\delta^{18}\text{O}$ values of xylem water in willow plants over the course of the summer (Singer et al. 1998). Sedge plants exhibited a seasonal enrichment and plants located adjacent to streams had $\delta^{18}\text{O}$ values of xylem water that were significantly ($P < 0.01$) depleted compared with plants in upland locations in June and September (Fig. 8).

Our mixing model analyses showed that three-quarters (mean = 77%; se = 4.5%) of willow plant water

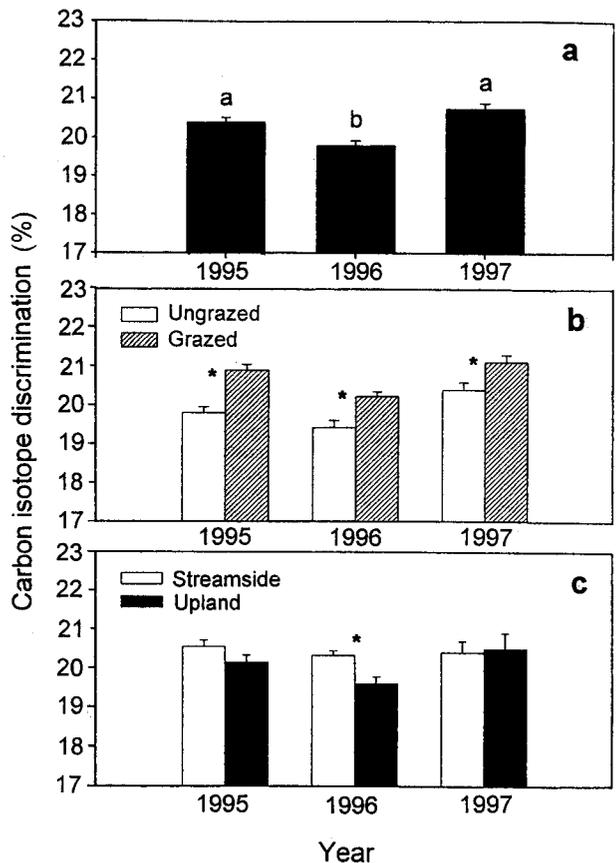


Fig. 6. *Salix monticola* leaf carbon isotope discrimination (LCID) values (mean and S.E.) based on plant collections late in the growing season (September) for 1995, 1996, and 1997 (a); late season LCID in ungrazed and grazed plants in 1995, 1996, 1997 (b); and late season LCID for plants located either streamside or in upland positions for 1995, 1996, and 1997 (c). Different letters indicate significant differences, $P < 0.05$, between years and an * indicates significant differences between ungrazed or grazed plants or between plants located streamside or in upland positions.

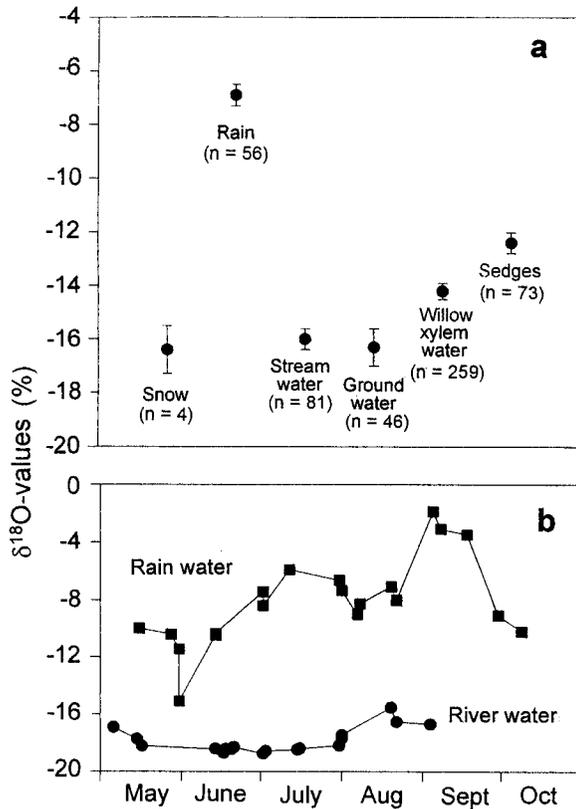


Fig. 7. $\delta^{18}\text{O}$ -values of *Salix monticola*, and *Carex* spp. xylem water, snow, rain, stream, and groundwater in Moraine Park, (1995, 1996, and 1997 combined) (a) and summer rain $\delta^{18}\text{O}$ -values versus stream water $\delta^{18}\text{O}$ -values during the 1997 growing season (b).

was derived from stream water/groundwater in these systems and only one-fourth (mean = 23%; se = 3%) of their water came from summer rain. In contrast, sedge reliance was significantly ($P < 0.01$) greater on summer rain (45%; se = 4%) while obtaining the other one-half of their water from groundwater (55%; se = 3%).

Discussion

We initially anticipated that winter grazing by elk would be detrimental to the physiological performance of willow, reducing rates of gas exchange, for example. We also anticipated that increases in stream water levels in short-watered willow sites would have a positive effect on willow carbon and water relations and that both willow and associated graminoid species would be competing for similar water resources in these riparian

habitats. However, we found that in general, most of our measures of willow physiological performance were enhanced by winter grazing by elk and that the improvements in gas exchange (Δ) were most likely due to increases in stomatal conductance as opposed to an increase in photosynthetic rates. Under the mesic conditions of our study (snowfall and precipitation similar to the 30 year average in all years) the changes in surface water that we experimentally induced were not of a magnitude to elicit a consistent shift in willow carbon and water relations, though we would anticipate in years when snowpack and runoff are low, damming would have significant effect on the carbon and water relations of willow, especially late in the summer. In addition, our water source ($\delta^{18}\text{O}$) data indicates that willow and the surrounding graminoids (sedge) do not use an identical mix of water sources and thus, competition for water may not be a factor which is curtailing the growth, development and regeneration of willow in these montane riparian habitats.

Generally, willow stem water potentials were high (-0.8 MPa) for both 1995 and 1996, reflecting the mesic nature of these ecosystems in contrast to woody plant water potentials in more arid regions (Gordon et al. 1989; Welker and Menke 1990; Momen et al. 1992), though we did observe higher stem water potentials in grazed willow plants relative to ungrazed plants in 1996 which is consistent with earlier studies of woody species (Welker and Menke 1990) and graminoid responses to grazing (Toft et al. 1987; Day and Detling 1994). The proposed mechanism by which grazed plants have higher water potentials is an increase in the root to shoot ratio of grazed plants whereby canopies are fairly smaller relative to their root biomass (McNaughton 1983; Wright et al. 1989). The effect of grazing on willow water potentials was, however, not consistent between 1995 and 1996 due possibly to the variation in snowfall timing and dissipation and surface water run-off patterns (Fig. 1). The significant increase in stem water potentials of the grazed willow plants in the second year may have resulted from the dependence of this response on a drier overall annual hydrologic regime, especially the diminished stream flows late in the summer (Singer et al. 1997, 1998).

The nitrogen content of willow leaves ranged between 3.2% and 2.2% over the entire growing season (Fig. 5), and were generally higher than other N values reported for willow leaves from other montane ecosystems (Singer et al. 1994; Dernburg 1997; Phillips 1997), though they were within the range reported by Phillips (1997). Winter grazing by elk did, however, cause an

Table 1. $\delta^{18}\text{O}$ -values (mean and SE) for *Salix monticola* stem water from riparian areas of the elk winter range in Rocky Mountain National Park, 1995 and 1996.^a

Source water	1995		1996		1995 and 1996 combined	
	Mean	SE	Mean	SE	Mean	SE
Streamside	-14.4	(0.6)	-14.4	(0.3)	-14.4 ^{a,b}	(0.4)
Upland	-12.5	(0.9)	-14.6	(0.3)	-13.6	(0.3)
Grazed	-12.2	(1.1)	-15.2	(0.5)	-13.7	(0.4)
Ungrazed	-13.8	(0.5)	-15.0	(0.4)	-15.0	(0.4)
Average	-12.9	(0.5)	-14.8	(0.2)	-14.2	(0.3)

^aValues are relative to Standard Mean Oceanic Water (SMOW).

^bMeans were not significantly different ($P < 0.05$).

increase in the N content of leaves, though the effects were not consistent over the entire growing season. Only in June was leaf N of grazed plants significantly higher than for ungrazed plants (Fig. 5). This lack of a consistent effect was not surprising as the ungrazed treatment actually represented the removal of grazing of willow plants by elk in our enclosure, just one year before our physiological measurements. The inconsistency of a short-term response of changes in leaf N associated with herbivory does not, however, preclude a long-term

change in leaf mineral nutrition and associated processes. In grazed grasslands, grasses consumed by herbivores consistently have higher leaf nitrogen than ungrazed plants (Ruess et al. 1983; Ruess and McNaughton 1984; Jaramillo and Detling 1992), resulting from a more juvenile nature of leaf tissue in grazed grasses that had higher N content (Ruess et al. 1983; Wallace et al. 1984; McNaughton et al. 1988) and from herbivore inputs of urea and feces which may increase the soil N content and thus increase the availability of N for plants (Floate 1981; Ruess and McNaughton 1984; Wallace et al. 1984; Jaramillo and Detling 1992).

Willow leaf carbon isotope discrimination (Δ) was significantly higher for grazed as opposed to ungrazed plants in all years, contrary to our instantaneous gas exchange measures (Fig. 6). These increases in integrative leaf gas exchange indicate that over the course of the entire growing season, grazed plants may have had consistently higher intercellular CO_2 concentrations (Ehleringer et al. 1992). These differences in apparent carbon gain attributes induced by grazing may or may not correspond to differences in growth and reproduction, though higher LCID values were associated with higher water potentials in grazed as compared to ungrazed plants.

Higher rates of LCID values and associated higher rates of stomatal conductance could be due to reductions in leaf area associated with grazing without reductions in root biomass (McNaughton 1983). This could result in a shift in the root to shoot ratio, whereby acquisition of soil water and nutrients were distributed over a smaller canopy volume, altering gas exchange. This improvement in both the intrinsic and extrinsic conditions of grazed plants had been reported for graminoid species (Caldwell et al. 1981; McNaughton

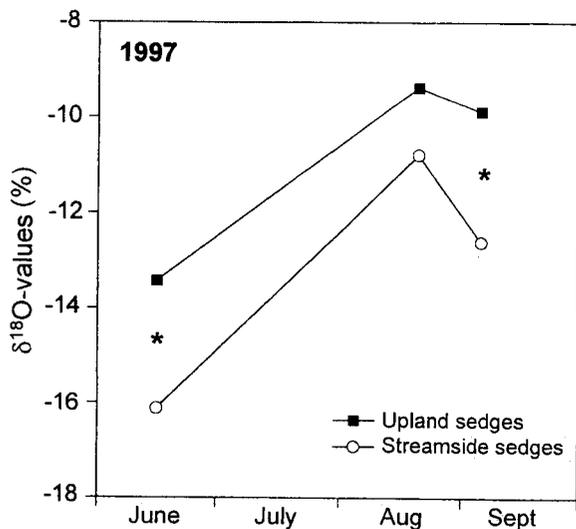


Fig. 8. $\delta^{18}\text{O}$ -values of sedge plants over the summer (1997) that were either streamside or in upland positions (mean and S.E.). An * indicates significant differences between landscape positions ($P < 0.05$).

1983) and less frequently for woody plants (Heichel and Turner 1983; Welker and Menke 1990; Houle and Simard 1996). Landscape position of willow plants across our valley floodplains also significantly influences LCID with streamside plants having higher Δ values than those plants that are in upland positions away from active stream channels (Fig. 6c). The higher rates of carbon isotope discrimination in streamside plants is likely due to greater access to streamwater which resulted in greater rates of stomatal conductance and higher C_i/C_a ratios (Ehleringer and Cooper 1988; Farquhar et al. 1989). Higher leaf carbon isotope discrimination of streamside plants as opposed to upland willow plants indicated that plants from streamside positions should have had either lower rates of photosynthesis or higher rates of stomatal conductance relative to the upland plants. However, photosynthesis was not different between streamside and upland plants. Thus, greater carbon isotope discrimination for streamside plants was probably caused by higher rates of stomatal conductance.

One would assume that higher rates of conductance would be associated with higher total plant water potentials in streamside plants. However, no significant differences were found in water potentials for plants from the two locations, suggesting that there existed a decoupling of total plant water status and stomatal conductance. Alternatively, plants near the streams may experience higher atmospheric humidity and thus lower vapor pressure deficits that should enhance stomatal conductance and subsequent carbon isotope discrimination (Schulze et al. 1987).

The mean xylem water $\delta^{18}\text{O}$ values of willow plants shifted very little over the course of the growing season, and were consistently close to that of streamwater averaging -14%. The slight enrichment from -16% to -14% for willow plants indicated the use of summer rain, but only to a small extent (~25%) indicating that streamwater was the dominant source of water used by willow. In contrast, sedge $\delta^{18}\text{O}$ values were much closer to that of summer rain on average (Fig. 7). However, sedge plants do exhibit a seasonal enrichment as their reliance on summer rain progressively increases and sedge plants close to stream channels make greater use of streamwater than plants in upland locations, which utilize summer rain to a greater degree (Fig. 8).

These differences in source water utilization between the graminoid and woody life forms in our riparian ecosystem are likely based in part on rooting

characteristics, including root form and distribution. Grasses typically have fibrous root systems concentrated in part close to the soil surface providing a mechanism whereby they may utilize light summer showers (Sala and Lauenroth 1982; Dodd et al. 1998). Woody plants, including willow and cottonwood species, often have roots at depths providing access to deeper water sources, typically untapped by surrounding herbaceous vegetation, resulting in the spatial partitioning of soil resources (Walter 1979). Soil resource partitioning is typically hypothesized to occur only in semi-arid settings (Gordon et al. 1989; Dodd et al. 1998), though our study suggests that even in mesic habitats, different life forms may utilize different water source combinations.

Landscape position appeared not to influence the water source used by willow (Table 1). In general, the stream water is infiltrating the vadose zone across the entire riparian floodplain and the small difference in microtopography (<1.0 m) associated with streamside and upland plants was not enough to significantly affect the water source, especially in wet years. Ground water use, regardless of proximity to existing stream channels, was consistent with the findings of Dawson and Ehleringer (1991) in a riparian plant water-use study that showed that streamside trees used ground water throughout the season. This observation was also seen with boxelder (*Acer negundo* L.) trees in a montane riparian system in Arizona (Kolb et al. 1997). Deep root systems in these cases supplied the majority of the water regardless of proximity to stream channels.

In summary, the carbon and water relations of willow were significantly affected by winter grazing by elk and in some cases by landscape position with regards to proximity to active stream channels. Grazing of willow by elk increases plant water potentials and integrative measures of gas exchange (Δ), though grazing did not consistently affect instantaneous rates of photosynthesis or the sources of water used by willow as measured by the $\delta^{18}\text{O}$ values of xylem water. It appears that under the mesic conditions of our study, grazing may have a positive effect on carbon and water relations of willow, and that competition for water sources with surrounding graminoids may not be severe and may not hinder willow water acquisition or carbon fixation. Under drier conditions (low snowpack and low stream flow), however, willow plants will likely experience water stress and increased competition for water with herbaceous neighbors, leading to reductions in willow carbon

fixation. Decreases in carbon gain may in turn lead to reductions in grazing resistance which would threaten the regeneration of *S. monticola* in these ecosystems.

Acknowledgments

This research was funded by a USGS-BRD research award to: F. J. Singer, J. M. Welker, E. T. Elliott, M. C. Coughenour, and D. Valentine to study plant-animal interactions in Northern Rocky Mountain ecosystems. Support by the staff at Rocky Mountain National Park is gratefully acknowledged, especially T. Johnson, and C. Axtell. B. Peterson and D. Ruess of the Natural Resources Ecology Laboratory (NREL) also contributed significantly to this study. K.A. Alstad was a graduate student in the Rangeland Ecosystem Science Department at the time of the study.

Literature Cited

- Alstad, K. P. 1998. Seasonal patterns of *Salix* carbon and water relations: Effects of browsing and hydrologic conditions. Masters thesis, Department of Rangeland Ecosystem Science, Colorado State University, Fort Collins.
- Baron, J. 1992. Chapter 8. Surface waters. Pages 142–182 in J. Baron, editor. Biogeochemistry of a subalpine ecosystem: Loch Vale Watershed. Volume 70. Springer-Verlag, New York.
- Briske, D. D. 1986. Plant responses to defoliation: morphological considerations and allocation priorities. Pages 425–427 in P. J. Joss, P. W. Lynch, and O. B. Williams, editors. Rangelands: A resource under siege. Proceedings of the second international rangeland congress, Australian Academy of Sciences, Canberra, Australia.
- Busch, D. E., and S. D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. Ecological Monographs 65:347–370.
- Busso, C. A., and J. H. Richards. 1995. Drought and clipping effects on tiller demography and growth of two tussock grasses in Utah. Journal of Arid Environment 29:239–251.
- Caldwell, M. M., J. H. Richards, D. A. Johnson, R. S. Nowak, and R. S. Dzurec. 1981. Coping with herbivory: Photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. Oecologia 50:14–24.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78:1958–1965.
- Chapin III, S. F., A. J. Bloom, C. B. Field, and R. H. Waring. 1987. Plant responses to multiple environmental factors. Bioscience 37:49–56.
- Coughenour, M. B., S. J. McNaughton, and L. L. Wallace. 1985. Responses of an African tall-grass (*Hyparrhenia filipendula* staph.) to defoliation and limitations of water and nitrogen. Oecologia 68:80–86.
- Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. Geochemica Et Cosmochimica Acta 12:133–149.
- Dawson, T. E. 1993. Water sources of plants as determined from xylem water isotopic composition: Perspectives on plant competition, distribution, and water relations. Pages 465–496 in J. R. Ehleringer, A. E. Hall, and G. D. Farquhar, editors. Stable isotopes and plant carbon-water relations. Academic Press, San Diego, Calif.
- Dawson, T. E., and J. R. Ehleringer. 1991. Streamside trees that do not use stream water. Nature 350:335–337.
- Dawson, T. E., and J. S. Pate. 1996. Seasonal water uptake and movement in root systems of Australian phreatophytic plants of dimorphic root morphology: A stable isotope investigation. Oecologia 107:13–20.
- Day, T. A., and J. K. Detling. 1994. Water relations of *Agropyron smithii* and *Bouteloua gracilis* and community evapotranspiration following long-term grazing by prairie dogs. American Midland Naturalist 132:381–392.
- Dernburg, A. R. 1997. Cattle preferences for willow (*Salicaceae*) in a montane riparian site. Ph.D. Colorado State University, Ft. Collins.
- Detling, J. K., and E. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. Oecologia 41:127–134.
- Dodd, M. B., W. K. Lauenroth, and J. M. Welker. 1998. Differential water resource use by herbaceous and woody plants in a shortgrass steppe community. Oecologia 117(4):504–512.
- Donovan, L. A., and J. R. Ehleringer. 1994. Carbon isotope discrimination, water-use efficiency, growth, and mortality in a natural shrub population. Oecologia 100:347–354.
- Ehleringer, J. R. 1991. $^{13}\text{C}/^{12}\text{C}$ fractionation and its utility in terrestrial plant studies. Pages 187–200 in carbon isotope techniques. Academic Press Inc., San Diego.

- Ehleringer, J. R., and T. A. Cooper. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* 76:562–566.
- Ehleringer, J. R., and T. E. Dawson. 1992. Water uptake by plants: Perspectives from stable isotope composition. *Plant, Cell and Environment* 15:1073–1082.
- Ehleringer, J. R., and C. B. Osmond. 1989. Stable isotopes. Pages 281–300 in R. W. Pearcy, J. R. Ehleringer, H. A. Mooney, and P. W. Rundel, editors. *Plant physiological ecology. Field methods and instrumentation*. Chapman and Hall, London.
- Ehleringer, J. R., S. L. Phillips, and J. P. Comstock. 1992. Seasonal variation in the carbon isotope composition of desert plants. *Functional Ecology* 6:396–404.
- Epstein, S., and T. Mayeda. 1953. Variations of ^{18}O content of water from natural sources. *Geochimica Et Cosmochimica Acta* 42:213–224.
- Evans, J. R., T. D. Sharkey, J. A. Berry, and G. D. Farquhar. 1986. Carbon isotope discrimination measured concurrently with gas exchange to investigate CO_2 diffusion in leaves of higher plants. *Australian Journal of Plant Physiology* 13:281–292.
- Fahnestock, J. T., and J. K. Detling. 1999. Plant responses to defoliation and resource supplementation in the Pryor Mountains. *Journal of Range Management* 52(3):263–270.
- Farquhar, G. D., M. C. Ball, S. von Caemmerer, and Z. Roksandic. 1982. Effect of salinity and humidity on $\delta^{13}\text{C}$ value of halophyte - Evidence for diffusional isotope fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO_2 under different environmental conditions. *Oecologia* 52:121–124.
- Farquhar, G. D., J. R. Ehleringer, and K. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40:503–537.
- Feild, T. S., and T. E. Dawson. 1998. Water sources used by *Didymopanax pittieri* at different life stages in a tropical cloud forest. *Ecology* 1448–1452.
- Floate, M. J. S. 1981. Effects of grazing by large herbivores in agricultural ecosystems. Pages 585–601 in F. E. Clark and T. Rosswall, editors. *Terrestrial nitrogen cycles: Process, ecosystem strategies and management impacts*. Volume 33. *Ecological Bulletin*, Swedish Natural Science Research Council, Stockholm.
- Gat, J. R. 1980. The isotopes of hydrogen and oxygen in precipitation. Page 21 in P. Fritz and J. Ch. Fontes, editors. *Handbook of environmental isotope geochemistry*. Elsevier Scientific Publishing Company, New York.
- Georgiadis, N. J., R. W. Ruess, S. J. McNaughton, and D. Western. 1989. Ecological conditions that determine when grazing stimulates grass production. *Oecologia* 81:316–322.
- Gleick, P. H. 1998. Water in crisis: Paths to sustainable water use. *Ecological Applications* 8:571–579.
- Gordon, D. R., J. M. Welker, K. J. Rice, and J. W. Menke. 1989. Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. *Oecologia* 79:533–541.
- Heichel, G. H., and N. C. Turner. 1983. CO_2 assimilation of primary and regrowth foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): Response to defoliation. *Oecologia* 57:14–19.
- Houle, G., and G. Simard. 1996. Additive effects of genotype, nutrient availability and type of tissue damage on the compensatory response of *Salix planifolia* spp. to simulated herbivory. *Oecologia* 107:373–378.
- Jaramillo, V. J., and J. K. Detling. 1992. Small scale heterogeneity in a semi-arid North American grassland. I. Tillering, N uptake and retranslocation in simulated urine patches. *Journal of Applied Ecology* 29:1–8.
- Kolb, T. E., S. C. Hart, and R. Amundson. 1997. Boxelder water sources and physiology at perennial and ephemeral stream sites in Arizona. *Tree Physiology* 17:151–160.
- LECO. 1993. CHN-1000 Elemental Analyzer Instruction Manual Version 1.4. LECO Corp., St. Joseph, Missouri.
- McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40:329–336.
- McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. *Bioscience* 38:794–800.
- Momen, B., J. W. Menke, and J. M. Welker. 1992. Tissue water relations *Quercus wislizenii* seedlings: Drought resistance in a California evergreen oak. *Acta Ecologica* 13:127–136.
- Naiman, R. J., C. A. Johnston, and J. C. Kelly. 1988. Alteration of North American streams by beaver. *Bioscience* 38:753–762.
- Naiman, R. J., G. Pinay, C. Johnston, and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. *Ecology* 75:905–921.
- Naiman, R. J., J. Magnuson, D. McKnight, J. Stanford, and J. Karr. 1995. Freshwater ecosystems and their management: A national initiative. *Science* 270:584–585.

- Naiman, R. J., J. J. Manuon, and P. L. Firth. 1998. Integrating cultural, economic and environmental requirements for fresh water. *Ecological Applications* 8:569–570.
- O'Leary, M. H. 1981. Carbon isotope fractionation in plants. *Phytochemistry* 20:553–567.
- Ott, L. 1993. An introduction to statistical methods and data analysis. Fourth edition. Duxbury Press, Belmont, Calif.
- Pimentel, D., J. Houser, E. Preiss, O. White, H. Fang, L. Mesnick, T. Barsky, S. Tariche, J. Schreck, and S. Alperr. 1997. Water resources: Agriculture, the environment, and society. *Bioscience* 47:97–106.
- Potvin, C., M. J. Lechowicz, and S. Tardif. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology* 71:1389–1400.
- Phillips, R. 1997. Forage quality as affected by previous cattle use in a montane riparian ecosystem. M.S. thesis, Colorado State University, Ft. Collins.
- Ruess, R. W., and S. J. McNaughton. 1984. Urea as a primitive coupler of plant-herbivore interactions. *Oecologia* 63:331–337.
- Ruess, R. W., S. J. McNaughton, and M. B. Coughenour. 1983. The effects of clipping, nitrogen source and nitrogen concentration on the growth responses and nitrogen uptake of an East African sedge. *Oecologia* 59:253–261.
- Sala, O. E., and W. K. Lauenroth. 1982. Small rainfall events, an ecological role in semi arid regions. *Oecologia* 53:301–304.
- SAS Institute, Inc. 1995. SAS user's guide. Release 6.11. SAS Institute Inc., Cary, NC.
- Schulze, E. D., R. H. Robichaux, J. Grace, P. W. Rundel, and J. R. Ehleringer. 1987. Plant water balance. *Bioscience* 37:30–37.
- Singer, F. J., L. C. Mack, and R. G. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. *Journal of Range Management* 47:435–443.
- Singer, F., T. Elliot, M. Coughenour, J. Welker, S. Williams, R. Peinetti, R. Menezes, L. Zeigenfuss, K. Alstad, D. Barnett, D. Valentine, R. Cates, and J. Zou. 1997. Large mammalian herbivores, plant interactions and ecosystem processes in five national parks – second annual report. Cooperative Agreement 1445-0009-94-1074, Subagreement 2. U.S. Geological Survey, Biological Resources Division. Ft. Collins, Colo.
- Singer, F., T. Elliot, M. Coughenour, J. Welker, S. Williams, R. Peinetti, R. Menezes, L. Zeigenfuss, K. Alstad, D. Barnett, D. Valentine, R. Cates, and J. Zou. 1998. Large mammalian herbivores, plant interactions and ecosystem processes in five national parks – third annual report. Cooperative Agreement 1445-0009-94-1074, Subagreement 3. U.S. Geological Survey, Biological Resources Division. Ft. Collins, Colo.
- Svejar, T. J., and J. D. Trent. 1995. Gas exchange and water relations of Lemmon's willow and Nebraska sedge. *Journal of Range Management* 48:121–125.
- Toft, N. L., S. J. McNaughton, N. J. Georgiadis. 1987. Effects of water stress and simulated grazing on leaf elongation and water relations of an East African grass, *Eustachys paspaloides*. *Australian Journal of Plant Physiology* 14:211–226.
- U.S. Department of Agriculture, Snow Survey Office. 1995, 1996, 1997. Snowpack data for Rocky Mountain National Park. National Resources Conservation Service. Lakewood, Colo.
- Wallace, L. L., S. J. McNaughton, and M. B. Coughenour. 1984. Compensatory photosynthesis responses of three African graminoids to different fertilization, watering, and clipping regimes. *Botanical Gazette* 145:151–156.
- Walter, H. 1979. *Vegetation of the earth*. Springer-Verlag, New York.
- Welker, J. M., and D. D. Briske. 1992. Clonal biology of the temperate caespitose graminoid *Schizachyrium scoparium*: A synthesis with reference to climate change. *Oikos* 56:357–365.
- Welker, J. M., and J. W. Menke. 1990. The influence of simulated browsing on tissue water relations, growth and survival of *Quercus douglasii* (Hook and Arn.) seedlings under slow and rapid rates of soil drought. *Functional Ecology* 4:807–817.
- Welker, J. M., D. R. Gordon, and K. J. Rice. 1991. Capture and allocation of nitrogen by *Quercus douglasii* seedlings in competition with annual and perennial grasses. *Oecologia* 87:459–466.
- Welker, J. M., D. D. Briske, and R. W. Weaver. 1987. Nitrogen-15 partitioning within a three-generation tiller sequence of the bunchgrass *Schizachyrium scoparium*: Response to selective defoliation. *Oecologia* 24:330–334.
- Welker, J. M., E. J. Rykiel, D. D. Briske, and J. D. Goeschl. 1985. Carbon import among vegetative tillers within two bunchgrasses: Assessment with carbon-11 labeling. *Oecologia* 67:209–212.
- Welker, J. M., T. H. E. Heaton, B. Spiro, and T. V. Callaghan. 1995. Indirect effects of winter climate on the delta $\delta^{13}\text{C}$ and the delta dD characteristics of

- annual growth segments in the long-lived, arctic plant *Cassiope tetragona*: A preliminary analysis. *Paleoclimatology Research* 15:105–120.
- Welker, J. M., U. Molau, A. N. Parsons, C. H. Robinson, and P. A. Wookey. 1997. Responses of *Dryas octopetala* to ITEX environmental manipulations: A synthesis with circumpolar comparisons. *Global Change Biology* 3(1):61–73.
- Wright, S. L., R. W. Hall, and J. W. Peasock. 1989. Effect of simulated insect damage on growth and survival of northern red oak (*Quercus rubra* L.) seedlings. *Environmental Entomology* 18:235–239.