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Anna Sala
University of Montana - Missoula, sala@mso.umt.edu

Robert S. Nowak

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ECOPHYSIOLOGICAL RESPONSES OF THREE RIPARIAN GRAMINOIDS TO CHANGES IN THE SOIL WATER TABLE

ANNA SALA[1] AND ROBERT S. NOWAK

Division of Biological Sciences, University of Montana, Missoula, Montana 59812; and Department of
Environmental and Natural Resources, University of Nevada, Reno, Nevada 89557

We examined the effect of changes in soil water table on the water relations, leaf gas exchange, and aboveground biomass of three riparian graminoids native to the semiarid western United States: Carex lanuginosa, Juncus balticus, and Carex nebrascensis. All three species co-occur at the wettest microhabitats within riparian corridors, but J. balticus and C. nebrascensis extend into drier areas. Lowering the water table to 1 m had little effect on the leaf gas exchange characteristics of the three graminoids. In the greenhouse, experimental reductions of the water table when plants had three fully mature leaves did not affect gas exchange rates or water potential in any of the three species. Lowering the water table when plants had one fully mature leaf resulted in limited differences between plants grown under high and low water table in J. balticus and C. lanuginosa. Further, these differences were only apparent after long periods of depressed water table (19 wk). In the field, rates of leaf gas exchange did not differ between plants growing near the creek from those occurring distant from the creek. Three factors contribute to the ability of these riparian graminoids to maintain favorable gas exchange and water relations across a range of water table depths. Each species appears to adjust rooting depth to, or just above, the shallow saturated zone. In the field, C. nebrascensis and J. balticus exhibited reductions of aboveground live biomass at locations far from the creek compared to those near the creek. Small adjustments of osmotic potential and the bulk modulus of elasticity help cells of C. nebrascensis and J. balticus maintain turgor as water table drops during the season. The limited distribution of C. lanuginosa near the creek may result, in part, from a higher biomass allocation to leaves and a less efficient water transport from roots to leaves, particularly when depressions of the water table occur during early growth stages.

Introduction

Riparian areas are key ecological interfaces between terrestrial and fresh water ecosystems (Carter 1986). Although limited in area (Knopf et al. 1988), riparian ecosystems in arid and semiarid regions have substantial ecological and economic value because they provide habitat for wildlife (Knopf et al. 1988; Szaro 1989), recreation areas, forage for livestock, and water resources for downstream communities. The ecological and economic importance of riparian areas in arid and semiarid areas, coupled with the extensive alteration of riparian ecosystems (e.g., dams, diversions), and associated with increasing population pressure, has motivated substantial ecological research in these systems.

The high productivity and species diversity of riparian zones in arid and semiarid regions, relative to adjacent upland zones (Mitsch and Gosselink 1986), are often attributed to abundant soil water availability. Although it is generally assumed that wetland plants are completely dependent on immediate access to a shallow water table, spatial and temporal fluctuations of the water table and of soil water availability in semiarid regions are common and may strongly influence plant production. With few exceptions (Ratliff and Westfall 1988, 1992; Svejcar and Trent 1995), the effects of temporal (i.e., occurring at different growth stages) and spatial variation of water table on the growth and physiological performance of graminoid

[1]Author for correspondence and reprints. Fax 406-243-4184; E-mail sala@selway.umt.edu.

riparian species are not well documented. Such information is critical to evaluate potential consequences of water table fluctuations and/or of changes in land management of riparian ecosystems.

The purpose of this study was to examine the effect of changes in soil water table on the growth and physiological performance of three graminoids native to western U.S. riparian meadows: Carex lanuginosa Michx., Carex nebrascensis Dewey, and Juncus balticus Willd. We also examined how these responses vary depending on the growth stage at which the depression of the water table occurs.

Material and methods

Carex lanuginosa, Carex nebrascensis, and Juncus balticus co-occur at the wettest microhabitats within the riparian corridor, but only J. balticus and C. nebrascensis extend into drier areas farther from the stream. Field observations of plant water relations, leaf gas exchange, and aboveground biomass were made along transects perpendicular to the stream as well as during experimental manipulations of soil water table for plants grown in a greenhouse.

GREENHOUSE EXPERIMENTS

The response of C. lanuginosa, C. nebrascensis, and J. balticus to decreased water table was experimentally tested in a greenhouse experiment at the University of Nevada, Reno, during 1992. Monocultures of each species were established in November 1990 by transplanting individual tillers into 280-L barrels (0.6 m diameter $\times$ 0.9 m high) filled with a dry, uniform, loamy sand (Kolseth et al. 1994). Water table depth and plant growth stage were controlled from March to July 1992. Water table depth was maintained at 0.15 and 0.75 m below the soil surface, using a mariotte bottle system (Parshall 1937). Water table depth was set when plants had one fully mature leaf (one-leaf) and when

plants had at least three mature leaves (three-leaf). A split-split-plot experimental design was used, with species as the main plot factor, with the growth stage treatment randomly assigned to subsets of barrels within each species and with the water table treatments randomly assigned to subsets within each growth stage. The overall experiment had three species, two growth stages, two water table treatments, and three replicates per cell, for a total of 36 barrels.

Plants in each barrel were clipped to 0.10 m in height 3 wk prior to treatments, and soils were brought to full saturation. Water table depth was then maintained at 0.15 m below the soil surface. On March 6, 1992, plants reached the one-leaf growth stage and the water table treatment was applied on assigned barrels. The desired water table (0.75 m) was reached within 1 wk after the beginning of the treatment. The remaining barrels were maintained at 0.15 m until plants reached the three-leaf growth stage (April 1), at which time the remaining barrels were subjected to their respective water table treatment. Water table depth was periodically verified with observation wells placed in each barrel.

Diurnal courses of leaf water potential, photosynthetic rate, leaf conductance, and leaf transpiration during clear weather conditions were conducted after 2, 7, and 19 wk from the beginning of the water table treatment imposed at the one-leaf growth stage and after 2, 4, and 15 wk for the three-leaf growth stage. Weather conditions did not permit comparable measurement intervals for the two growth stage treatments. Diurnal measurements were always made on the two youngest, fully mature leaves of a randomly selected tiller per barrel (i.e., three replicates per treatment) at ca. 2-h time intervals. Bulk leaf water potential was measured with a Scholander-type pressure chamber (Turner 1988). Stomatal conductance and photosynthetic rates were measured with a closed portable photosynthesis system (LiCor 6200, LiCOR Inc., Lincoln, Nebr.). Transpiration rates were calculated from measurements of leaf conductance coupled with independent measurements of leaf temperature and air vapor pressure that were taken with the cuvette open. Instantaneous water use efficiency (WUE) was calculated as the ratio of photosynthesis to calculated transpiration. One-side leaf area inside the cuvette was calculated from accurate measurements of leaf and cuvette width. For *J. balticus,* which has circular leaves, one-side leaf area was corrected by multiplying the projected leaf area by $\pi/2$.

The slope of the linear relationship between instantaneous transpiration rates and xylem water potential was used as an estimate of the ability of the soil-plant hydraulic system to supply water to leaves (Elfving et al. 1972; Küppers et al. 1987). Within a species and growth stage, comparisons between water table treatments were done by pooling the data from all measurement days. Although the slope varied from day to day, comparisons done on a daily basis yielded similar results as with pooled data.

Relative water content of the soil was measured 2 and 15 wk after the water table treatments were initiated at each of the two growth stages. Measurements were made at 0.2, 0.4, and 0.6 m below the soil surface with a neutron probe (Model H503 Hydroprobe, Campbell Pacific Nuclear, Martinez, Calif.). Neutron probe access tubes were in the center of each barrel, and the neutron probe was calibrated against gravimetric measures of soil water content prior to the experiment (Kolseth et al. 1994).

At the end of the experiment, total aboveground green biomass in each barrel was clipped to 0.10 m in height and harvested. Biomass was dried at 70°C for 3 d and then weighed.

Greenhouse results were analyzed with split-plot and split-split-plot ANOVA models (SAS Institute 1989). For data sets where comparisons between growth stages were appropriate, a split-split-plot model was used with species as the main plot factor, growth stage as the subplot factor, and water table depth as the sub-subplot factor. For data sets where comparisons between growth stages were not appropriate, a split-plot ANOVA was used, with species as the main-plot factor and water table depth as the subplot factor.

FIELD STUDIES

STUDY AREA. The field study was conducted from May to August 1992 at Big Grizzly Creek (39°56′N, 120°37′W, 1740 m elevation), in the eastern Sierra Nevada, ca. 90 km northwest of Reno, Nevada. The riparian meadow consists of graminoid species with *Carex* and *Juncus* as major species. A mixed conifer forest with a primary overstory of *Pinus contorta* and *Pinus ponderosa* and a primary understory of *Artemisia tridentata* and *Purshia tridentata* occurred in the areas upland from the edge of the meadow. *Carex nebrascensis* and *J. balticus* occurred from the creek to the forest edge, whereas *C. lanuginosa* was found only in and along the creek. Three transects perpendicular to the creek were established for the field experimental design. Along each transect, measurements were made at two locations: next to the creek (no farther than 0.5 m) and near the forested edge of the riparian meadow (ca. 75 m from the creek). Water table depth was measured periodically on observation wells installed to ca. 1.3 m at each meadow location and transect. We were unable to determine water table depth after it dropped below 1.3 m.

Long-term (47 yr) average annual temperature and precipitation at the closest National Climate Data Center official weather station, Portola, California (39°48′N, 120°28′W, 1478 m elevation), are 8°C and 564 mm, respectively. During 1992, mean daily temperature at Portola was ca. 3°C warmer than the long-term average for May, but it was within 1°C for June–August. Precipitation for the period of May–August 1992 at Portola (135 mm) was over twice the long-term average (63 mm), but May was drier than average, whereas June, July, and August were much wetter than average. During the 1992 field study period, mean daily temperature at Big Grizzly Creek averaged ca. 3.5°C lower than at Portola. Precipitation at Big Grizzly Creek for the May–August period (71 mm) was slightly greater than the long-term average for Portola. Most of the precipitation at Big Grizzly Creek came in June (55 mm), with a 25-mm storm on June 5 and a 16-mm storm on June 28.

ECOPHYSIOLOGICAL MEASUREMENTS. Leaf ecophysiological measurements along the three transects were made periodically during the growing season on three consecutive days. Sampling periods were May 13–15, May 26–28, June 17–19, July 7–9, and July 20–22, 1992. Weather during each 3-d measurement period was clear, with similar diurnal temperatures among the three consecutive sampling days. The only exception was the June 17–19 sampling period, where all 3 d were overcast. Diurnal courses of leaf gas exchange and leaf water potential were derived from measurements taken every 2 h on three randomly selected tillers for each species and location along a transect. Because early-morning frost and dew prevented accurate predawn readings, the earliest measurement of leaf water potential took place at 500 hours solar time. Although sunrise occurred up to 2 h earlier, the trees and mountains to the east of the riparian meadow

effectively shaded the plots until after the first set of water potential measurements were completed. Measurements of bulk leaf water potential and leaf gas exchange characteristics were performed as described above in the greenhouse experiments.

Bulk tissue water relations were determined from pressure-volume curves (Tyree and Hammel 1972) of leaf samples that were collected at each location along each transect. Leaf samples were collected in June (early season samples), late July (*J. balticus*), and mid-August (*C. nebrascensis* and *C. lanuginosa*); late July and mid-August samples will be referred to as late season samples. (*Juncus balticus* was sampled earlier than the *Carex* species because it exhibited obvious symptoms of senescence; additional samples of *J. balticus* were taken in mid-August, but because of advanced senescence, the pressure-volume procedure was not possible.) Three mature leaves per species and meadow location (one per transect) were collected between 500 and 700 hours solar time and placed inside several layers of plastic bags with a moist paper towel. Once in the laboratory, leaves were allowed to rehydrate in the refrigerator for ca. 30–45 min to avoid overhydration (Meinzer et al. 1988; Kubiske and Abrams 1991). Preliminary trials confirmed that this rehydration time was the maximum before inducing an initial plateau in the pressure volume curve, which is often associated with tissue overhydration (Kubiske and Abrams 1991). Pressure volume data analysis was done using the "PVC" model described by Schulte and Hinckley (1985). The parameters derived from the analysis are osmotic potential at full saturation (Π_{sat}), osmotic potential at the turgor loss point (Π_{ppt}), relative water content at the turgor loss point (RWC_{tlp}), and maximum bulk modulus of elasticity (ϵ_{max}).

Because of the unbalanced experimental design (*C. lanuginosa* was present only at one location along the meadow transects), a series of split-plot ANOVAs (SAS Institute 1989) were used to analyze the data. A split-plot ANOVA was used to analyze species (main plot) and date during the growing season (subplot) differences at each individual meadow location. Similarly, a split-plot ANOVA was used to analyze meadow location (main plot) and date (subplot) differences for each of the two species *J. balticus* and *C. nebrascensis*. Statistical analyses excluded data collected during the overcast period in mid-June. Species differences in pressure-volume parameters were analyzed with a separate two-way ANOVA for each meadow location. A three-way ANOVA was used to analyze meadow location differences for *C. nebrascensis* and *J. balticus*.

Results

GREENHOUSE

The growth stage at which the water table was lowered did not influence soil water content in any of the three species studied. Thus, data for the two growth stage treatments were pooled for further analyses. The experimental decrease of the water table to 0.75 m significantly reduced soil water availability in the upper parts of the soil profile (0.2 and 0.4 m) for all three species and in the lower part of the soil profile (0.6 m) only for *Juncus balticus* (fig. 1). These differences were significant after 2 and 15 wk of treatment. After 15 wk of treatment, *J. balticus* barrels subjected to low water tables had very low soil water content at all
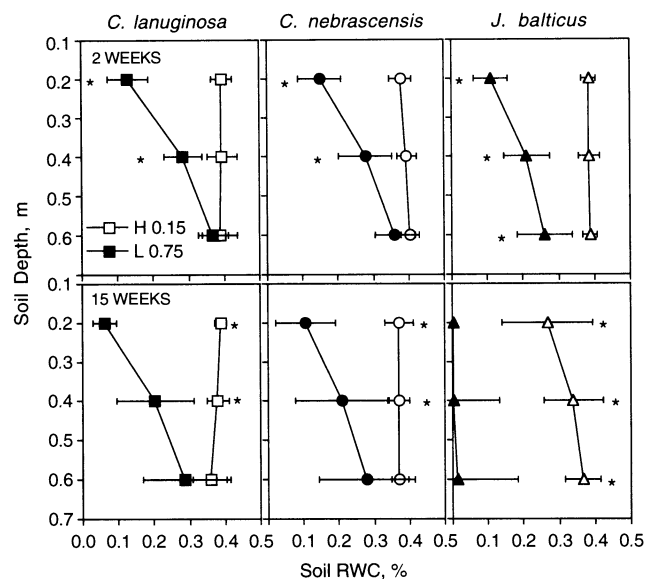
Fig. 1 Soil relative water content at 0.2, 0.4, and 0.6 m below the soil surface in *Carex lanuginosa*, *Carex nebrascensis*, and *Juncus balticus* barrels subjected to high water table (open symbols) or low water table (filled symbols). Measurements were taken 2 wk and 15 wk after the water table treatments were applied and are pooled for the one- and three-leaf phenological stages. Error bars are standard deviation of the mean. Stars denote water table treatment differences within a given soil depth.

depths, with values significantly lower than those measured for the two *Carex* species.

Photosynthesis rates, stomatal conductance, and transpiration rates on a leaf area basis were relatively constant during the day for all three species. Most of the variation resulted from variation in incident radiation. For simplicity, only maximum values that occurred at highest irradiance were used.

Lowering the water table at the one-leaf growth stage did not affect leaf gas exchange and water potential in any of the species for the first 7 wk (fig. 2). This lack of response persisted in *Carex nebrascensis* during the entire length of the experiment. In contrast, after 19 wk of lowered water table, leaves of *Carex lanuginosa* and *J. balticus* from plants grown with a low (0.75 m) water table had significantly lower stomatal conductance and transpiration rates, but not photosynthesis, than plants grown with a high (0.15 m) water table (fig. 2). In both species, instantaneous water use efficiency increased in the low water table treatment, but not in a statistically significant manner. In general, water table depth did not affect leaf water potential in any of the three species (fig. 2).

Lowering the water table at a later growth stage (three-leaf) did not affect gas exchange characteristics or leaf water potential during the entire duration of the experiment (15 wk; fig. 2).

The growth stage at which the water table was lowered did not affect gas exchange characteristics and water potential measured after 2 wk of lowered water table. Further comparisons were not possible because
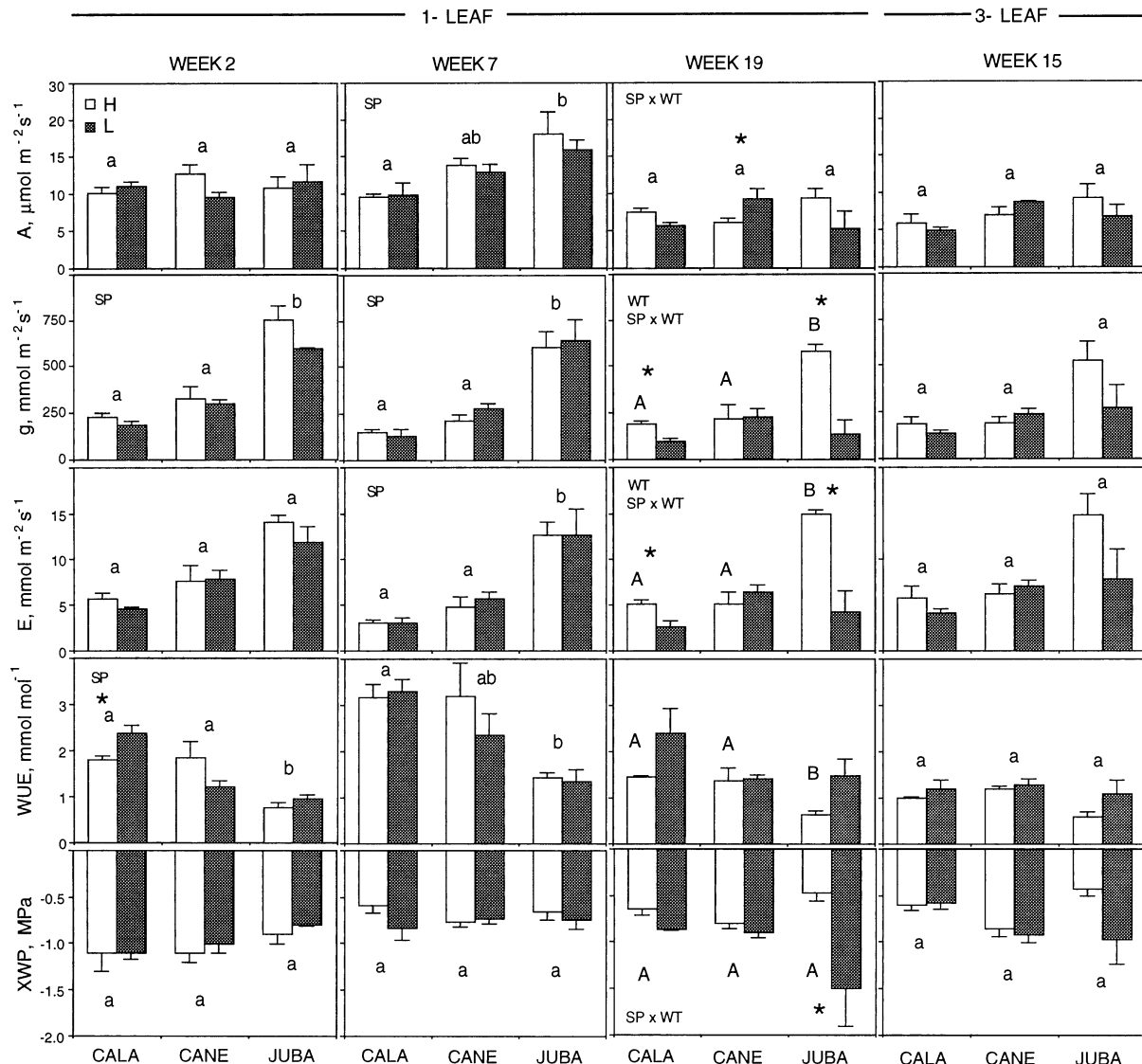
Fig. 2 Stomatal conductance (*g*), photosynthesis rates (*A*), transpiration rates (*E*), water use efficiency (*WUE*), and leaf xylem water potential (*XWP*) measured from 1200 to 1400 hours, solar time, in *Carex lanuginosa* (*CALA*), *Carex nebrascensis* (*CANE*), and *Juncus balticus* (*JUBA*) in the greenhouse after 2, 7, and 19 wk of water table treatment applied when plants had one fully developed leaf (1-leaf) and after 15 wk of water table treatment applied when plants had three fully developed leaves (3-leaf). Open bars denote high water table (0.15 m) and shaded bars, low water table (0.75 m). Error bars are standard error of the mean (n = three barrels per treatment with three leaves per barrel). Within a given date, overall significance between species (*SP*), water table (*WT*), and their interaction (*SP* × *WT*) are indicated in each panel (split-plot ANOVA, *P* < 0.05). Stars denote significant water table treatment differences within a species and date (LSD, *P* < 0.05). Within each date overall species differences are indicated by different lowercase letters. Capital letters indicate species differences when comparing only the high water table treatment (*P* < 0.05).

measurement intervals varied for the two growth stage treatments.

Species comparisons were done separately for the two growth stages, but the analyses yielded similar results. Stomatal conductance and transpiration rates of *J. balticus* were generally higher than those of the two *Carex* species (fig. 2). Net photosynthesis was similar among the three species. Consequently, water use efficiency was, in general, significantly lower in *J. balticus* than in the two *Carex* species (fig. 2).

Instantaneous transpiration rates were significantly correlated with xylem water potential for the two *Car-*

ex species under both water table treatments and leaf growth stages, but not for *J. balticus* (table 1). At the one-leaf growth stage, the slope of this relationship for *C. lanuginosa* plants grown at low water tables was significantly higher than that of plants grown at high water tables. However, at the three-leaf growth stage, the slope in *C. lanuginosa* did not change in response to lowering the water table. In *C. nebrascensis* there were no changes in the slope resulting from water table depth at either growth stage.

At the end of the experiment, only *J. balticus* sub-jected to a low water table exhibited substantial se-

Table 1

SLOPES OF THE LINEAR RELATIONSHIP BETWEEN PAIRED MEASURE-
MENTS OF XYLEM LEAF WATER POTENTIAL AND TRANSPIRATION
RATES IN *CAREX LANUGINOSA*, *CAREX NEBRASCENSIS*, AND
JUNCUS BALTICUS IN THE GREENHOUSE EXPERIMENTS

Species	Treat-ment	Slope	r^2	n
C. lanuginosa, one-leaf	H	1.27[a]	0.47	58
	L	1.85[b]	0.51	51
C. nebrascensis, one-leaf	H	0.87[a]	0.42	58
	L	0.89[a]	0.48	50
J. balticus, one-leaf	H	7.16	0.02[ns]	40
	L	0.19	0.06[ns]	57
C. lanuginosa, three-leaf	H	0.81[a]	0.31	45
	L	0.88[a]	0.36	45
C. nebrascensis, three-leaf	H	0.78[a]	0.40	45
	L	0.79[a]	0.55	45
J. balticus, three-leaf	H	0.17	0.19[ns]	43
	L	0.11	0.05[ns]	33

Note. Measurements were done on plants that had been subjected
to two water table treatments (H = 0.15 m and L = 0.75 m) after
they had one fully developed leaf (one-leaf) or three fully developed
leaves (three-leaf). Slopes were obtained by pooling all the data
collected during the experiment. Also indicated are r^2 and n. All
regressions are significant ($P < 0.02$), except when indicated with
ns. Within each species, different letters indicate significant treat-
ment differences ($P < 0.01$).

nescence compared with the high water table treat-
ment. In contrast, no visually detectable differences in
senescence were observed in the two *Carex* species.
Accordingly, green aboveground biomass for *J. balti-
cus* was reduced with the lowered water table treat-
ment in both growth stages (statistically significant
when the two growth stages were combined), but
aboveground biomass in the water table treatments for
the two *Carex* species was not significantly different
(fig. 3).

FIELD STUDIES

Along the creek, the depth to water table decreased
from 0.4 m at the beginning of May to about 1 m at
the end of the season (fig. 4). At the forest edge, water
table depth dropped rapidly from 1 m to over 1.3 m
and remained at or below 1.3 m to the end of the
season.

Seasonal trends of daily maximum values of sto-
matal conductance, photosynthesis rates, and transpi-
ration rates were similar among the three species (fig.
5). While near the creek, maximum stomatal conduc-
tance and photosynthesis rates in all three species de-
creased significantly during the growing season (fig.
5), values at the forest edge remained relatively con-
stant. The increase in maximum stomatal conductance
and photosynthesis rates observed in *J. balticus* at both
meadow locations at the end of July resulted from the
fact that most mature individuals had senesced and
measurements were restricted to young leaves that
emerged following June rain events. Transpiration
rates remained constant over the season at the creek
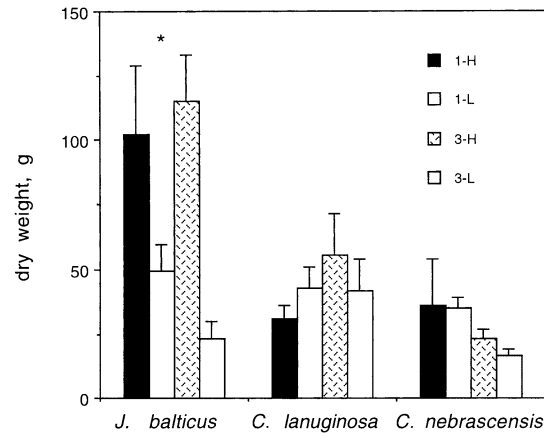and increased by the end of the season at the forest

Fig. 3 Total biomass per barrel of the three species at the end of
the greenhouse experiments. Data are shown for each phenological
stage (*1* = one fully mature leaf; *3* = three fully mature leaves) and
water table depths (*H* = high, 0.15 m; *L* = low, 0.75 m) treatments.
Significant differences between the high and low water table treat-
ments when data for the two phenological stages were combined are
indicated by an asterisk.

edge (fig. 5). *Carex nebrascensis* and *J. balticus* ex-
hibited a significant decline in instantaneous WUE
(measured at the time of maximum transpiration) dur-
ing the season regardless of meadow location (fig. 5).
Early-morning measurements of leaf water potential
remained relatively constant during the growing sea-
son at the creek but declined slightly at the forest edge
(fig. 5). Minimum leaf water potentials on clear days
were highest early in the season, decreased by late
May (significantly at the forest edge; fig. 5), and re-
mained low thereafter. Cloudy and rainy weather in
June greatly increased minimum plant water potential
for all species.

Maximum stomatal conductance, photosynthesis
rates, and transpiration rates during clear days were
consistently higher and WUE was lower in *J. balticus*
compared with the two *Carex* species (fig. 5). Leaf
water potentials early in the morning at the creek lo-
cation were similar in all species, but minimum values
tended to be lower in *C. lanuginosa*.
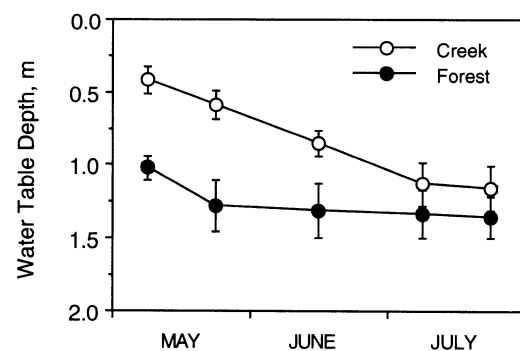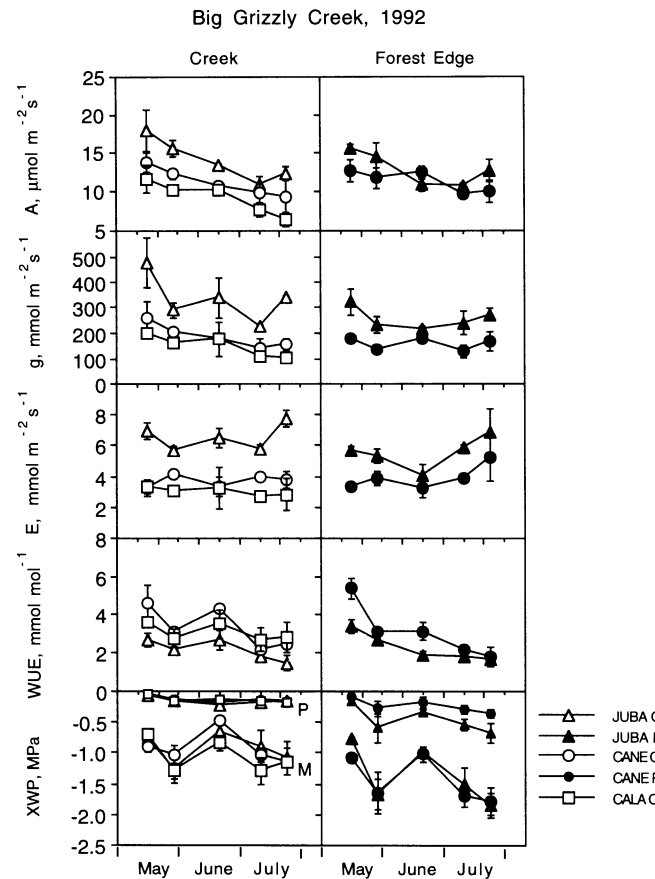
Gas exchange characteristics of *C. nebrascensis* and

Fig. 4 Depth to the water table at the creek (open symbols) and
forest edge (solid symbols) locations. Error bars are 1 standard error
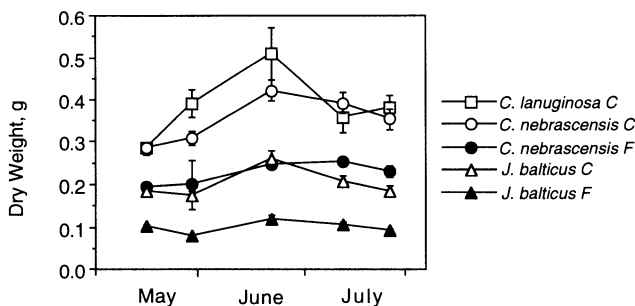of the mean (*n* = three wells per meadow location).

Big Grizzly Creek, 1992

Fig. 5 Seasonal course of maximum stomatal conductance (g), photosynthesis (A), transpiration (E), water use efficiency at the time of maximum transpiration rates (WUE), and early-morning (P) and minimum (M) leaf xylem water potential (XWP) at the creek and forest edge locations. Measurements were made for *Carex lanuginosa* $(CALA)$, *Carex nebrascensis* $(CANE)$, and *Juncus balticus* $(JUBA)$. Error bars are 1 standard error of the mean $(n =$ three transects perpendicular to the stream, with three replicate individuals per transect and location).

J. balticus were little affected by the meadow location (fig. 5). In early May, differences in leaf water potential between the two meadow locations were also insignificant even though the water table was significantly lower at the forest edge. Later in the season, minimum leaf water potential in both species was generally lower at the forest edge than at the creek (fig.

Fig. 6 Changes in aboveground tiller (for *Carex* species) or leaf (for *Juncus*) green biomass during the season at the creek (open symbols) and forest edge (solid symbols) locations in the field. Values in each location are means of three transects with five individuals per species and transect. Error bars are 1 standard error.

5), but differences were only significant for *C. nebrascensis*.

Biomass per tiller for the *Carex* species and leaf biomass of *J. balticus* increased until mid-June and early July and decreased thereafter at the creek location (fig. 6). At the forest edge, biomass of *C. nebrascensis* and *J. balticus* showed little variation during the growing season (fig. 6). Biomass of these two species was significantly lower at the forest edge than at the creek.

The osmotic potential at full saturation and at the turgor loss point for *C. nebrascensis* and *J. balticus* significantly decreased from early to late in the season at the creek $(P < 0.001)$, but remained unchanged at the forest edge $(P > 0.05;$ table 2). Differences resulting from meadow location were only apparent early in the season $(P < 0.05)$. No significant seasonal changes in osmotic potential were observed in *C. lanuginosa*. A strong decrease of ϵ_{max} from early to late in the season was observed in *C. nebrascensis* and *J. balticus* $(P < 0.002)$, but not in *C. lanuginosa* (table 2). The relative water content at the turgor loss point was similar in the three species and did not change

Table 2

MEAN ($\pm$SE) OSMOTIC POTENTIAL AT FULL SATURATION (Π_{sat}), AT THE TURGOR LOSS POINT (Π_{tlp}) AND
BULK MODULUS OF ELASTICITY (ϵ_{max}) DERIVED FROM PRESSURE VOLUME CURVES PERFORMED FOR
CAREX LANUGINOSA (CALA), *CAREX NEBRASCENSIS* (CANE), AND *JUNCUS BALTICUS* (JUBA) AT
THE CREEK AND FOREST EDGE LOCATIONS (ALL UNITS ARE MPA)

	Creek			Forest edge	
	CALA	CANE	JUBA	CANE	JUBA
Π_{sat}:					
Early	−1.3 (.13)[a]	−1.4 (.14)[a]	−1.5 (.02)[a]	−1.7 (.09)[a]	−2.2 (.11)[a]
Late	−1.7 (.15)[a]	−2.0 (.08)[b]	−1.9 (.12)[b]	−1.8 (.10)[a]	−2.4 (.12)[a]
Π_{tlp}:					
Early	−1.7 (.16)[a]	−1.7 (.14)[a]	−2.3 (.10)[a]	−2.4 (.13)[a]	−3.1 (.23)[a]
Late	−2.2 (.19)[a]	−2.9 (.17)[b]	−2.8 (.49)[a]	−2.7 (.14)[a]	−2.9 (.14)[a]
ϵ_{max}:					
Early	9.4 (.72)[a]	19.0 (2.5)[a]	13.5 (1.1)[a]	19.9 (4.7)[a]	22.5 (2.4)[a]
Late	8.3 (.55)[a]	7.5 (1.0)[b]	5.9 (.15)[b]	6.6 (.73)[b]	11.5 (1.9)[b]

Note. Measurements were taken early (early June for all three species) and late in the season (late July for *J. balticus*; mid-August for the two *Carex* species). Within a given species, different letters denote significant seasonal changes ($P < 0.05$).

throughout the season or from the creek to the forest edge (overall averages $\pm$ SE were 85.5 $\pm$ 2.2, 86.8 $\pm$ 2.6, and 83.5 $\pm$ 3.4 for *C. lanuginosa, C. nebrascensis,* and *J. balticus,* respectively).

Discussion

The limited effects of the water table depth on the gas exchange characteristics in the studied species are related, in part, to their rooting characteristics. Although root activity and root biomass of *Carex nebrascensis*–dominated communities is typically concentrated in the upper 0.4 m of the soil profile (Manning et al. 1989; Svejcar and Trent 1995), our observations in the greenhouse and in the field indicate that the three graminoids are able to reach shallow groundwater (up to 1.3 m deep) or moist soil layers just above the shallow groundwater. Adjustment of rooting depth to access shallow water resources may enable the studied plants to satisfy a large proportion of the transpirational demand and thus minimize stomatal limitations of gas exchange.

Carex nebrascensis and *Juncus balticus* may also maintain favorable gas exchange under low water tables by reducing leaf area in drier habitats. In the field, live aboveground biomass of the two species was significantly reduced near the forest edge where the water table was lower. Similarly, in the greenhouse leaf biomass of *J. balticus* was significantly reduced when the water table was experimentally lowered. This was not the case for the two *Carex* species, which may result from a combination of factors, including higher water tables than those observed in the field and different soil characteristics. By reducing leaf area in drier habitats (and possibly by increasing the root-to-shoot ratio), water supply to shoots may be improved, thus minimizing decreases of stomatal conductance and photosynthesis rates throughout the growing season. Because live aboveground biomass per tiller was lower at the forest edge

than at the creek from the beginning of the growing season, prevailing lower water tables at the forest edge appear to have a long-term effect on the aboveground production of these graminoid species. Substantial interannual decreases of aboveground standing biomass concurrent with decreases in precipitation have also been reported in *C. nebrascensis*–dominated meadows of semiarid areas (Svejcar and Trent 1995). The extent to which reductions of aboveground biomass, whether from lowered water tables or from decreased precipitation, are reversible adaptive responses that allow riparian graminoid species of semiarid areas to persist through dry periods is not known. However, recent studies in mesic wetlands and mires have shown large decreases of *Carex* species cover after natural or anthropogenic declines of the water table (Jukaine and Laiho 1995; Kazda 1995), indicating that community shifts occurring in response to lowered water table result partly from the sensitivity of *Carex* species to depressed water tables. Overall, our field data indicate that structural, rather than functional, adjustments are the most important mechanism by which these graminoids cope with depressed water tables. In the long term these structural changes at the individual scale may result in cover changes at the community scale.

Changes in tissue elasticity and solute concentration are other mechanisms by which plants subjected to drought are able to maintain turgor and ensure survival (Munns 1988). *Carex nebrascensis* and *J. balticus* adjusted solute concentrations to some degree at the creek but not at the forest edge, which may be related to the larger seasonal decreases in water table at the creek than at the forest edge. It may also be related to the fact that at the creek, aboveground biomass decreased significantly after June, which may have contributed to increased solute concentration in the remaining biomass, leading, in turn, to an increase of the osmotic potential (Munns 1988). Although the

rain in June prevented severe water deficits, a substantial increase in tissue elasticity was observed in C. nebrascensis and J. balticus but not in Carex lanuginosa. Seasonal increases in tissue elasticity may enable the species with broader distribution to maintain turgor and to survive during periods of severe drought and deep water table.

Of the three species, only C. lanuginosa exhibited a change in the leaf specific resistivity when subjected to lowered water table at the one-leaf growth stage. This indicates that when water table is lowered at an early growth stage, root development in unsaturated soil layers and growth toward the water table may limit the efficiency of the soil-plant hydraulic pathway. In the field, C. lanuginosa is only found near or in the creek where water tables are high during early stages of development. At this location C. lanuginosa exhibited the largest aboveground biomass and the largest decrease in live tiller biomass during the seasonal decrease of the water table. Minimum leaf water potential of C. lanuginosa tended to be lower than in C. nebrascensis and J. balticus in spite of the fact that transpiration rates were lower in C. lanuginosa than in the other two species. Overall, these results indicate that the limited distribution of C. lanuginosa to near the creek may be due, in part, to higher biomass allocation to leaves and a rather inefficient hydraulic pathway that is unable to supply the transpirational demand when the water table, particularly during early stages of development, decreases beyond a critical point.

Seasonal decreases of maximum stomatal conductance observed in the three species were not accompanied by parallel decreases of leaf water potential (which remained constant since mid-May). Rather, decreases in stomatal conductance paralleled concurrent decreases of photosynthesis, indicating a dependency of stomatal conductance on photosynthesis (Ball et al. 1987). Since leaf nitrogen strongly influences photosynthesis in many species including wetland graminoids (Field and Mooney 1986; Konings et al. 1989; Pons et al. 1993) and seasonal decreases of leaf nitrogen have been documented in these graminoid species (Ratliff and Westfall 1988; Seeger 1993), the observed decrease of photosynthesis is likely a result of decreased leaf nitrogen.

Apparently, seasonal decreases of stomatal conductance were not sufficient to compensate for the seasonal increase in leaf-to-air vapor pressure difference. Transpiration rates remained constant or increased (at the forest edge) by the end of the season. As a result, the instantaneous WUE (at maximum transpiration rates) during clear days declined during the season for all three species. In contrast to the common pattern of an increase of WUE in species located on ridges compared to arroyos (Ehleringer and Cooper 1988; Mooney et al. 1989), WUE was not different between the creek and forest edge locations.

Acknowledgments

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