Oecologia (2012) 168:11–22
DOI 10.1007/s00442-011-2065-2

PHYSIOLOGICAL ECOLOGY - ORIGINAL PAPER

The effect of hydraulic lift on organic matter decomposition, soil nitrogen cycling, and nitrogen acquisition by a grass species

Cristina Armas · John H. Kim · Timothy M. Bleby · Robert B. Jackson

Received: 23 January 2010 / Accepted: 23 June 2011 / Published online: 16 July 2011

Abstract Hydraulic lift (HL) is the passive movement of water through plant roots, driven by gradients in water potential. The greater soil–water availability resulting from HL may in principle lead to higher plant nutrient uptake, but the evidence for this hypothesis is not universally supported by current experiments. We grew a grass species common in North America in two-layer pots with three treatments: (1) the lower layer watered, the upper one unwatered (HL), (2) both layers watered (W), and (3) the lower layer watered, the upper one unwatered, but with continuous light 24 h a day to limit HL (no-HL). We inserted ingrowth cores filled with enriched-nitrogen organic matter (^{15}N-OM) in the upper layer and tested whether decomposition, mineralization and uptake of ^{15}N were higher in plants performing HL than in plants without HL. Soils in the upper layer were significantly wetter in the HL treatment than in the no-HL treatment. Decomposition rates were similar in the W and HL treatments and lower in no-HL. On average, the concentration of NH_4^+-N in ingrowth cores was highest in the W treatment, and NO_3^--N concentrations were highest in the no-HL treatment, with HL having intermediate values for both, suggesting differential mineralization of organic N among treatments. Aboveground biomass, leaf ^{15}N contents and the ^{15}N uptake in aboveground tissues were higher in W and HL than in no-HL, indicating higher nutrient uptake and improved N status of plants performing HL. However, there were no differences in total root nitrogen content or ^{15}N uptake by roots, indicating that HL affected plant allocation of acquired N to photosynthetic tissues. Our evidence for the role of HL in organic matter decomposition and nutrient cycling suggests that HL could have positive effects on plant nutrient dynamics and nutrient turnover.

Keywords *Bouteloua dactyloides* · Decomposition · Hydraulic redistribution · Mineralization plant–soil water relations

Communicated by Jim Ehleringer.

C. Armas and J. H. Kim contributed equally to the paper.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-011-2065-2) contains supplementary material, which is available to authorized users.

C. Armas · J. H. Kim · R. B. Jackson
Department of Biology, Duke University,
Box 90338, Durham, NC 27708, USA

Present Address:
C. Armas (✉)
Estación Experimental de Zonas Áridas,
Consejo Superior de Investigaciones Científicas,
Carretera de Sacramento s/n, 04120 Almería, Spain
e-mail: cris@eeza.csic.es

T. M. Bleby
School of Plant Biology, The University of Western Australia
(M084), 35 Stirling Highway, Crawley, WA 6009, Australia

Introduction

Hydraulic redistribution (HR) is the phenomenon by which water moves passively from relatively moist to dry soil layers via plant root systems (e.g., Richards and Caldwell 1987). HR is driven by a gradient in soil water potential, with plant roots acting as conduits for water transport during HR. HR, and particularly hydraulic lift (HL) (when water moves from deep moist to shallow dry layers), are increasingly recognized as widespread phenomena, and we have a reasonably good understanding of where, when, and

how HR may occur (Dawson 1993; Jackson et al. 2000; Liste and White 2008). However, the full ecological consequences of HR are unclear.

Studies are now beginning to describe the ways in which plants can directly benefit from HR, and there is growing evidence that HR may be an ecologically important mechanism for some species and plant communities (Armas et al. 2010; Bleby et al. 2010; Jackson et al. 2000; Lee et al. 2005; Scott et al. 2008). For individual plants, the most obvious outcome of HR is that it moistens the rhizosphere around roots, keeping fine roots more hydrated when bulk soils are relatively dry (Valenzuela-Estrada et al. 2009) and in some cases increasing plant survival (Bauerle et al. 2008). HR in general, and HL in particular, also equalize spatially heterogeneous patches of soil moisture in surface soil layers (Burgess and Bleby 2006; Smart et al. 2005), and extend the period and area in which roots have access to water, particularly if rainfall can be redistributed for later use (Caldwell and Richards 1989). There is also evidence that HL can extend the activity and diversity of soil microorganisms and mycorrhizal networks in the root zone (Querejeta et al. 2003; Warren et al. 2008). HL can also promote greater rates of transpiration and photosynthesis in trees, and these processes continue for longer periods compared to when HL is absent (Bleby et al. 2010; Dawson 1997), potentially affecting community processes and even local climate (Lee et al. 2005). Overall, these benefits are thought to promote greater growth and survival, not only for plants that perform HL but also for their neighbors (Dawson 1993; Prieto et al. 2011).

In addition to its primary role of increasing soil moisture, HL has been suggested by numerous authors to be a potential mechanism to increase the availability of nutrients for plants (Caldwell et al. 1998; Caldwell and Manwaring 1994; Dawson 1993, 1997; Hawkins et al. 2009; Jackson et al. 2000; Liste and White 2008; Richards and Caldwell 1987; Rose et al. 2008; Smart et al. 2005; Snyder et al. 2008). Nutrients levels and rates of biogeochemical processes such as decomposition, mineralization, and nitrification are usually highest in the upper layers of soils, where biological and atmospheric inputs of nutrients to the soil are the greatest (Schlesinger 1997). However, as upper soil layers dry from evapotranspiration, nutrient mobility and availability to plants rapidly decrease. Clearly, additional inputs of water from HL have the potential to delay this decrease in soil nutrient mobility and availability.

Even in small amounts, HL seems capable of improving plant nutrient uptake in at least three ways. First, hydraulically lifted water may prolong the activity, extension, and life span of fine roots, root hairs and associated microorganisms such as mycorrhizae in dry surface soil (Bauerle et al. 2008; Querejeta et al. 2003). Secondly, water supplied by HL can improve ion mobility and diffusion to roots (Dawson 1997). Thirdly, water from HL may stimulate litter decomposition and microbial degradation of organic matter, as these processes are generally moisture-dependent (Aanderud and Richards 2009; Hawkins et al. 2009). Interestingly, inverse HL (downward HR) has also been implicated in nutrient uptake; McCulley et al. (2004) used nutrient concentration and stable isotope data to suggest that downward HR can promote the uptake of nutrients stored in deep, relatively dry soil layers where it is otherwise unavailable to most plants. The mobilization and redistribution of spatially distinct pools of nutrients and other elements via HR may also have broader consequences at the ecosystem level related to increased productivity (Liste and White 2008) and changes in hydrological and biogeochemical cycles (Aanderud and Richards 2009; Jackson et al. 2000; Jobbágy and Jackson 2004).

Theoretically, HL has significant potential to enhance litter decomposition, nutrient availability and nutrient uptake by plants. However, empirical evidence of these general processes is scarce, and in the specific case of nutrient uptake, the positive role of HL is not universally supported (Online resource 1). Several studies have considered the effect of HL on nutrients indirectly (Caldwell and Manwaring 1994; Crabtree et al. 1998; Dawson 1997; de Kroon et al. 1998; Hawkins et al. 2009; Huang 1999; Matzner and Richards 1996; Nambiar 1976; Rose et al. 2008; Snyder et al. 2008; Wang et al. 2009), but results have been largely inconclusive for a number of reasons, including lack of suitable control treatments, restricted experimental time scales, or addition of nutrients in aqueous solution rather than in solid form (see Online resource 1 for more details).

Here, we explored the direct role of HL in facilitating organic matter decomposition, nutrient mineralization, and plant nutrient acquisition by conducting a greenhouse experiment with plants of *Bouteloua dactyloides* (Nutt.) J.T. Columbus. We grew plants in pots with two hydrologically separated layers designed to permit hydraulic lift from 'deep' soil to 'shallow' soil under controlled conditions. Soil cores with organic matter (ground litter) enriched in ^{15}N were placed near shallow roots, and for 2 months plants were assigned to different watering and light treatments to allow or suppress HL. We hypothesized that: (1) plants performing HL would have relatively higher soil moisture in the shallow soils than the plants with HL suppressed; (2) higher soil moisture as a result of HL would enhance decomposition of the enriched ^{15}N litter and mineralization and mobility of the nutrients from this litter; (3) plants performing HL would acquire less ^{15}N than those plants regularly watered to saturation, but more ^{15}N than those with HL suppressed; and (4) plant biomass and physiological responses such as allocation to shoots, root

foraging in nutrient-enriched patches, and N content would reflect the water and nutrient status of plants from each treatment.

Materials and methods

The study species was Buffalo grass, *Bouteloua dactyloides*, a perennial deep-rooted grass species native to dry North American prairies (Plants of the Southwest, NM, USA). The strong seasonality of the climate in habitats where buffalograss is found and its root morphology both make HL a likely possibility for this species; it has a dense root system that thoroughly occupies the soil, including numerous thin roots $\sim$1 mm in diameter on average. In the field, its roots may reach soil layers 1.5 m below the surface, with 70% of roots by mass occurring in the top 15 cm of soil (Weaver 1958). Relatively deep wet soils, shallow drier soils and ranges of soil matric potential found in our study are commonly observed in buffalograss native habitats (Redmann 1978; Scanlon et al. 2005). Overall, *B. dactyloides* is a hardy species that is drought-, heat-, and cold-resistant, and it has been reported to facilitate HL (Huang 1999).

Plants were grown in two-layer cylindrical PVC pots that allowed watering of the bottom soil layer (75 cm high $\times$ 10 cm diameter) independently from the top soil layer (25 cm high $\times$ 10 cm diameter; Online resources 2–3). The soil layers were separated by a 0.5-cm-thick barrier, permeable to roots but not to water, which enabled us to isolate the effect of hydraulic lift by roots. The barrier was composed of a 3-mm mesh cloth soaked in a molten mixture of 1 part natural bee's wax (Yaley Enterprise n.110016, USA) and 1.5 part paraffin liquid (99% pure; Lamplight©, USA) that solidified after cooling. The barrier was carefully placed inside the PVC pot and a thin layer of silicone was used to seal the barrier to the inner walls of the pot.

Pots were filled with soils without nutrients, the bottom layer being fine river sand (Quikrete®, USA), whereas the top layer was filled with a mix of 1:3 (v/v) sand:fritted montmorillonite clay (Oil-Dri, MS, USA). The upper sand + fritted clay mixture was designed to provide good soil–root contact and a clear response to changes in soil water content and matric potential, as measured by thermocouple psychrometers described below.

In August 2007, 3-month-old buffalograss seedlings were transplanted to the experimental pots ($n = 18$), and grown for 10 additional months in a greenhouse (natural lighting, 20°C mean temperature) before beginning the experiment. The top and bottom layers of the pots were watered to saturation twice a week. Once a week, 60 ml of a modified Hoagland's solution low in nitrogen (0.5 mM N, mainly in the form of ammonium nitrate, NH_4NO_3; Online resource 4) was added to the bottom layer only. At the time of seedling transplant, the top layer of each pot was inoculated with 20 g of fresh soil from a grassland site at the Blackwood Division of the Duke Forest (35°58.8′′N, 79°5.37′′W).

Three months prior to the beginning of the experiment, we verified root growth into the bottom layer by visual observation of numerous roots growing up against small Perspex windows installed in modified pots (Online resource 3). The 18 vegetated pots were then moved into controlled growth chambers (20°C, relative humidity 85%, PAR 200 μmol $m^{-2}s^{-1}$, 14-h photoperiod) at the Duke University Phytotron. The plants were watered and supplied with nutrients as described above until the beginning of the experimental treatments. PAR intensity in all experimental chambers was intentionally relatively low, as most studies that apply continuous light cycles to plants (one of our treatments, see below) recommend low light intensity levels (<500 μmolm^{-2} s^{-1}), due to potential adverse effects of high-intensity continuous light on plants (Equiza et al. 2006; Velez-Ramírez et al. 2011; Xiao et al. 2007).

Experimental treatments

At the start of the experiment in June 2008, both upper and lower layers were watered to saturation. Twelve vegetated pots placed in one chamber were subjected to 12 h light/dark cycle (20°C, relative humidity 85%, PAR 200 μmolm^{-2} s^{-1}). Twice a week, six of these pots were watered to saturation, including both the top and the bottom layers (watered treatment, W). The other six pots were also watered twice a week in the bottom layer only (hydraulic lift treatment, HL). Six more vegetated pots were similarly watered twice a week in the bottom layer only and were placed in a second chamber with identical climatic conditions but with continuous 24-h light cycle to inhibit nightly stomatal closure and thus reduce or impair hydraulic lift (no hydraulic lift treatment, no-HL). Continuous illumination forces stomates to stay open at night, keeping the water potential gradient and flow of water from soil to plant to atmosphere instead of between soil layers through roots (Caldwell and Manwaring 1994). In each chamber, we also placed four additional pots as controls without plants but with bundles of dead grass on top (i.e., to simulate grass cover; note there were no roots inside these pots, only soil) to account for changes in soil moisture due to treatment–light cycle effects. These pots are denoted throughout the text as dead-plant controls or S12 and S24 treatments (for 12- and 24-h light cycle chambers, respectively).

Soil matric potential sensors (thermocouple psychrometers, model PST-55; Wescor, Logan, UT, USA) were used to monitor changes in soil moisture inside the pots. Psychrometers were installed in the upper and lower layers of each pot, at 15 and 60 cm depths, respectively. Psychrometers were interfaced with a datalogger (model CR7 + cooling current interface model A3497; Campbell Scientific, Logan, UT, USA), and soil matric potential was logged at 30-min intervals from the start of the experimental treatments. Psychrometers were calibrated against solutions of known concentrations of KCl following procedures in Brown (1970).

We also measured soil gravimetric water content of subsamples from soils collected at the end of the experiment. Samples were oven-dried at 80°C to a constant weight (expressed as g water/g soil ×100).

^{15}N-labeled organic material and experiments

Two weeks after the beginning of the experimental treatments (t_{15} in figures), we placed three ingrowth cores at 10 cm depth in the top layer of each pot: two ingrowth cores contained background soil mixed with ^{15}N-labeled ground litter as organic matter (OM-core) and the third contained background soil only (soil-only-core). The source of the OM enriched in ^{15}N was buffalograss leaves ground and oven-dried at 70°C (5.6 atom% ^{15}N, 3.0% N). The plants were grown from seed in a greenhouse with natural day/night air temperatures of 22/16°C and light levels of 1,000 μmol m^{-2} s^{-1}, with an 11-h photoperiod and an average humidity of 80%. Plants were well watered five times per week with distilled water and twice a week with 100 ml of a modified half-strength Hoagland's solution containing 0.8 g l^{-1} of $^{15}NH_4$ $^{15}NO_3$ (5 atom% ^{15}N; Isotec, Miamisburg, OH, USA). Aboveground biomass was harvested after 2.5 months and dried in an oven at 60°C. Plant material was then ground to make a coarse powder of organic matter enriched with ^{15}N.

The three ingrowth cores were designed to assess root growth, ^{15}N-OM decomposition rates and plant ^{15}N uptake in each treatment. The OM-cores consisted of 3 g of the wet sand + fritted clay mix plus 0.8 g of ^{15}N labeled organic matter housed in 3-cm^3 cylinders (length 63 mm; internal diameter 8 mm). The cylinders were made of a light plastic mesh with square pores 2–3 mm in size.

In August 2008, after 11 weeks of experimental treatment (9 weeks since the soil cores were placed in the pots), the buffalograss plants in our three experimental treatments were harvested. Aboveground material was separated into green leaves, dead leaves and runners or stolons. Belowground biomass was washed clean of soil and separated into four sample groups: roots from the top pot layer, the bottom pot layer, the ^{15}N-OM-core and the soil-only core. All samples were oven-dried at 70°C for 5 days. Green leaves, stolons and roots were ground, subsampled, and analyzed for C, N, and ^{15}N isotope contents. Soils from ingrowth cores were also analyzed for C and mineral N content (NH_4-N and NO_3-N). Soil samples from the OM-cores were also sampled prior to the start of the experiment and analyzed to acquire baseline levels of nutrients (t_{15} in figures).

Dried leaf, stolon, root, and soil samples were ground to a fine powder for C and N analyses. δ^{15}N was analyzed in leaves, stolons, and roots from the bottom layers and OM-ingrowth soil samples just before the ingrowth cores were first inserted into the pots (background values), and at the end of the experiment. C and N contents were determined with a Carlo Erba Elemental Analyzer, and δ^{15}N was measured in a Finnigan MAT Delta Plus XL continuous flow mass spectrometer system (Finnigan, San Jose, CA, USA), both at the Duke University Environmental Stable Isotope Laboratory (DEVIL). Mass spectrometer measurements had a precision of 0.2‰ for ^{15}N organic samples. The isotopic abundance was expressed in delta notation (δ) in parts per thousand (‰) as

$$\delta = \left(R_{\text{sample}}/R_{\text{standard}} - 1\right) \times 1000 \quad (1)$$

where R_{sample} and R_{standard} are the molar ratios of heavy to light isotope of the sample and the international standard (atmospheric N_2).

Percent of ^{15}N taken up by green leaves, stolons or roots from the ingrowth cores ($^{15}N_{\text{uptake}}$) was calculated as:

$$^{15}N_{\text{uptake}}(\%) = \left(^{15}N_{\text{tissue}}/^{15}N_{\text{cores}}\right) \times 100 \quad (2)$$

where $^{15}N_{\text{tissue}}$ is mg ^{15}N in the tissue at the end of the experiment minus background mg ^{15}N for each corresponding tissue, and $^{15}N_{\text{cores}}$ is mg ^{15}N of the OM-cores at the beginning of the experiment. Background δ^{15}N values for leaves, stolons and roots were −0.38 ± 0.15, −0.49 ± 0.15 and −0.63 ± 0.15‰, respectively.

Organic matter decomposition rates were expressed as the % C_{loss} month^{-1} and calculated as the difference in organic C in the OM ingrowth cores from the start to end of the experiment per unit of time (Aanderud and Richards 2009). Similarly, the difference between the initial and final NH_4^+ concentrations in the ingrowth cores per unit of time was considered to represent the net N mineralization of OM (Rice 2006); high estimated cation exchange capacity (CEC) of soil in upper layers (37.5 and 71.63 meq/100 g for soils in control and OM ingrowth cores, respectively) indicates that NH_4^+ was relatively immobile in those soils. Subsamples of 1 g of soil from the ingrowth cores were shaken in 20 ml 2 M KCl for NO_3^-

and NH_4^+ extractions, centrifuged, filtered, and analyzed using a QuikChem 8500 (Lachat Instruments).

Statistical analyses

Differences in plant responses and soil properties among treatments were tested using ANOVA at a significance level of $P < 0.05$, and homogeneity of variances was checked using Levene's test. Post-hoc differences were tested using HSD Tukey's or Tamahane's tests. Only the analyses for the following variables differed: differences among matric potentials of plant treatments during the course of the experiment were tested using RM-ANOVA and M-ANOVA at 0, 15, 30, 45, 60 and 75 days from the beginning of the experiment. Each matric potential value was the mean of 5 days around each specific date (the specific date plus 2 days on either side). Differences in the trend of observed soil matric potential among treatments were tested using ANCOVA with time (day) as the covariate. Psychrometer measurements near the end of the experiment (beyond day 60) were less definitive and were excluded from our analysis, as matric potential readings tended to converge as soil in the upper layers experienced severe drying at the end of the experiment. In the driest pots, some psychrometers also stopped functioning as soil matric potentials decreased to less than −6.0 MPa.

Throughout the experiment, the no-HL treatment and soil-only (no vegetation) pots were used as controls in our comparisons of matric potential, decomposition of ^{15}N-labeled litter, and ^{15}N uptake by the plants.

Relationships among soil water content, mineral N forms in ^{15}N-OM ingrowth cores, and plant traits were tested using linear correlation analyses. All statistical analyses were performed with the SPSS 17.0 (SPSS, IL, USA) or Statistica 9.0 software (StatSoft, OK, USA) and results throughout the text, tables and figures are presented as mean ± 1 SE.

Results

The matric potential of the upper soil layer in the well-watered treatment (W) was maintained near zero, while that of all other treatments steadily declined over the course of the 75-day experiment (Fig. 1a). Matric potential in the no-HL and the S24 (dead-plant control) treatments declined more rapidly than the HL and S12 treatments, and there was a clear divergence in the rate of decline in soil matric potential of plant treatments compared to their dead-plant controls (i.e. Fig. 1a; ANCOVA $F_{4,816} = 86.44$, $P < 0.001$; S24 and no-HL were not significantly different, $P = 0.50$, post-hoc-comparisons).

Apart from the W treatment pots, the wettest soil in the upper pot layer was consistently observed in the HL treatment. From day 20 until the end of the experiment, the matric potential of the upper soil layer of the HL treatment was on average 0.60 ± 0.02 MPa less negative (wetter) than that of its control (S12), 1.21 ± 0.10 MPa less negative than that of no-HL, and 1.51 ± 0.14 MPa less negative than that of S24 (Fig. 1a). This result illustrates that hydraulic lift maintained higher soil moisture in the HL treatment compared to the dead-plant control (S12) and other treatments. The differences in soil matric potentials in the upper soil layer between the HL and other treatments were statistically significant over the course of the experiment, as observed specifically on days 15, 30, 45 and 60 (Fig. 1b; RM-ANOVA $F_{26} = 36.02$, $P < 0.001$).

At the end of the experiment, the relative gravimetric water content of soil sampled from the soil-only ingrowth cores differed among treatments. Soil moisture in the HL treatment was half that of the W treatment but double that of the no-HL treatment (Table 1). The same treatment differences were observed for soil cores amended with the ^{15}N enriched organic matter (OM-cores), which were significantly wetter than soil-only cores. All these results were consistent with matric potential data, showing that our treatments produced the expected manipulation of hydraulic lift and soil moisture, increasing the soil water availability in the HL treatment compared to the no-HL treatment.

Although there were no differences in total soil N among the OM-cores of the different watering treatments at the end of the experiment, carbon contents in soils from OM-cores in the no-HL treatment were significantly higher than in the other treatments (W and HL, Table 1). Consequently, OM decomposition rates were similar in W and HL treatments but significantly lower in the no-HL treatment (Fig. 2; $F_{214} = 8.63$, $P < 0.01$; $P = 0.05$ for HL versus no-HL treatment, post-hoc comparisons), indicating that higher soil moisture increased OM decomposition.

The concentration of NH_4^+-N in soil from OM-cores at the end of the experiment (t_{75}) was significantly higher than the baseline level (t_{15}) in all treatments (Fig. 3a). The greatest increase in NH_4^+ was measured in the W treatment, followed by HL and then the no-HL, though the difference between the HL and no-HL treatments was not statistically significant for NH_4^+ (Fig. 3a) or for N mineralization (calculated from NH_4^+ values, data not shown). Pooling results across the three treatments, soil NH_4^+ was positively correlated with soil water content, decomposition rate, leaf N content and ^{15}N acquisition by plants (Table 2).

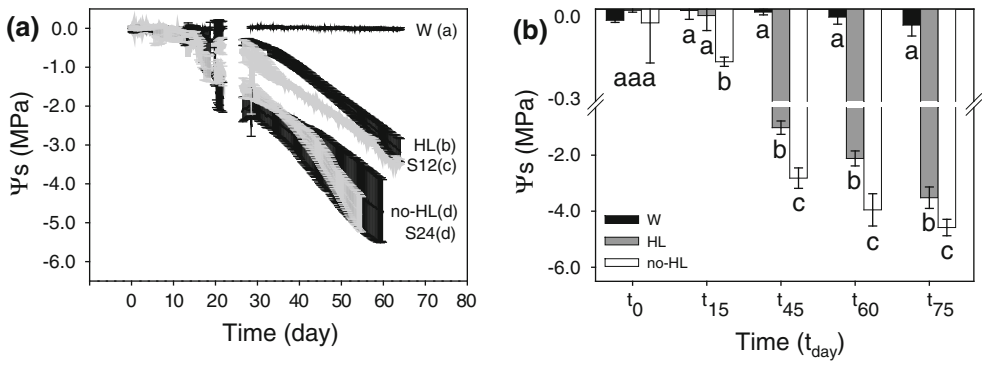

Fig. 1 The daily course of soil matric potential (Ψ_S) in the upper layer of pots from the start of the experiment until 3 weeks prior to plant harvest (**a**), and average Ψ_S on days 0, 15, 45, 60 and 75 (**b**). All data are mean ± SE of $n = 3$–4. *Different letters for lines* (**a**) and *bars* for each measurement date (**b**) denote significant differences at $P < 0.05$. Treatments are denoted for plant and soils under a 12/12-h day/night light cycle as: *W* all soil layers watered, *HL* lower soil layer watered, *S12* soil only; and for plant and soils under a 24-h light cycle: *no-HL* lower soil layer watered, *S24* soil only

Table 1 Parameters measured from ingrowth cores at the end of the experiment, including: gravimetric water content of soil (*Soil* soil-only cores, *OM* ingrowth cores with ^{15}N enriched organic matter), soil N and C content, root biomass inside the cores, and percentage of cores colonized by roots (mean ± 1SE; $n = 5$–6)

	W	HL	no-HL		*F*
Soil moisture (%)					
OM	90.15 ± 4.03 a	22.88 ± 0.53 b	12.99 ± 0.57 c	***	316.30***
Soil	47.17 ± 1.82 a	18.09 ± 0.30 b	10.84 ± 0.61 c		314.90***
Soil N (%)					
OM	0.26 ± 0.02 a	0.32 ± 0.04 a	0.34 ± 0.01 a	***	2.75 ns
Soil	0.01 ± 0.00 a	0.02 ± 0.01 a	0.02 ± 0.01 a		0.59 ns
Soil C (%)					
OM	4.51 ± 0.34 a	5.00 ± 0.71 a	7.07 ± 0.21 b	***	8.27**
Soil	0.15 ± 0.01 a	0.21 ± 0.00 a	0.23 ± 0.05 a		1.82 ns
Root biomass (g)					
OM	0.57 ± 0.32 a	3.42 ± 3.10 a	0.14 ± 0.08 a	ns	0.88 ns
Soil	0.80 ± 0.40 a	0.23 ± 0.15 a	0.21 ± 0.08 a		1.93 ns
Cores colonized (%)					
OM	71.43	85.71	71.43	ns	
Soil	71.43	28.57	71.43		

Treatments are denoted for plants under a 12/12-h day/night light cycle: *W* all soil layers watered, *HL* lower soil layer watered; and for plants under a 24-h light cycle: *no-HL* lower soil layer watered. Values in rows with different letters indicate significant differences among treatments at $P < 0.05$. Asterisks denote significant differences for a particular variable between control and ^{15}N enriched organic matter cores (**$P < 0.01$, ***$P < 0.001$, *ns* non-significant). Differences among treatments for the same variable and type of core were analyzed by ANOVA, and the resulting *F* value is shown in the last column. Differences between control and OM cores were analyzed by paired *t* test and the significance is shown in the second column from the right. The percentage of cores colonized by roots was analyzed by X^2 analysis

In contrast to the trend for NH_4^+, the concentrations of NO_3^- from the OM-cores at the end of the experiment (t_{75}) decreased significantly in all treatments compared to the baseline level (t_{15}). The W treatment showed the highest decrease in NO_3^- through time, followed by the HL treatment and then by the no-HL treatment (Fig. 3b). Also, in contrast to NH_4^+, NO_3^- was negatively correlated with relative soil water content, decomposition rate, live aboveground biomass and N content and ^{15}N acquisition by plants (Table 2), pointing to higher uptake or leaching of NO_3^- from the ingrowth cores in wetter soils maintained by hydraulic lift or frequent watering. Trends in the NH_4^+/NO_3^- ratio mirrored that of NH_4^+, except that the ratio in the HL treatment was significantly greater than in no-HL (Fig. 3c) and that correlations with other variables were tighter (Table 2).

Leaf $^{15}N_{uptake}$ in the HL treatment was 20 times higher (~0.41% of all the ^{15}N initially supplied as OM was found in the leaves; Fig. 4) than that of no-HL treatment (~0.02%). $^{15}N_{uptake}$ values were highest in W treatment

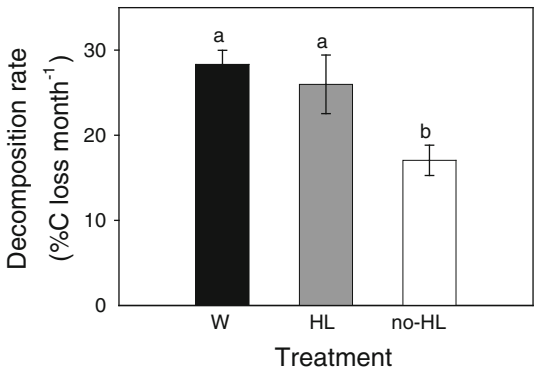

Fig. 2 OM decomposition rates in soils from the ^{15}N-OM-cores (mean ± 1SE; $n = 6$). *Bars with different letters* denote significant differences at $P < 0.05$. Legend as in Fig. 1

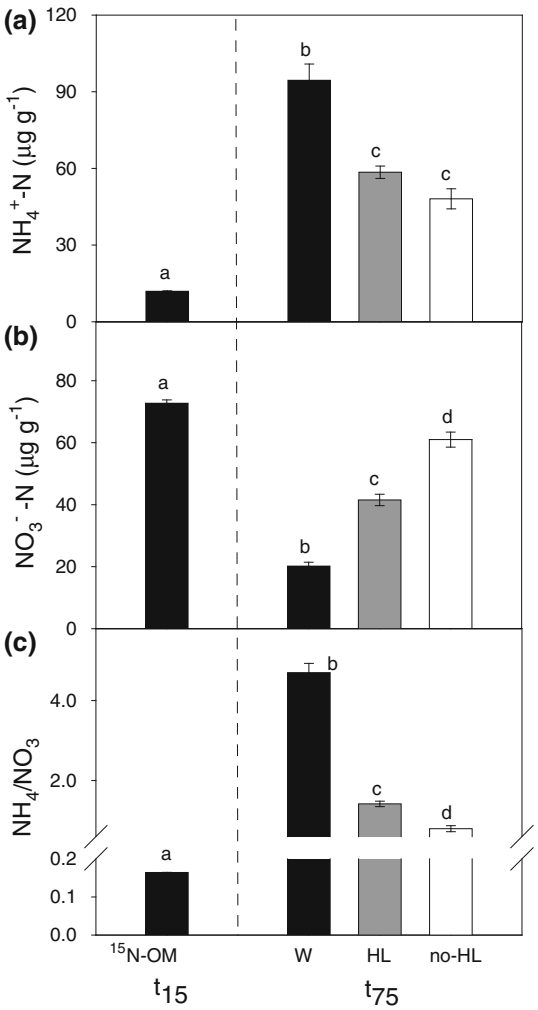

Fig. 3 NH_4 (**a**) and NO_3-N content (**b**), and NH_4 to NO_3 ratio (**c**) in soils from the ^{15}N-OM-cores when they were inserted in the pots (t_{15}) and at the end (t_{75}) of the experiment (mean ± 1SE; $n = 6$; only four samples at t_{15}). Units are µg of NH_4^+-N or NO_3^--N per g of soil (mix of fritted-clay, sand and OM). *Bars with different letters* denote significant differences at $P < 0.05$. Legend as in Fig. 1

(~6.17%), approximately 15 times higher than in HL treatment, and 300 times higher than in no-HL treatment ($F_{217} = 51.58$, $P < 0.001$). Leaf δ^{15}N showed similar differences among treatments (Table 3). Stolon and overall root $^{15}N_{uptake}$ did not differ among treatments (Fig. 4; Table 3; but see δ^{15}N values). Overall, these results suggest greater plant uptake and allocation to photosynthetic tissues of ^{15}N from the ingrowth cores in wetter soils maintained by either hydraulic lift or frequent watering than in the treatment where HL was inhibited.

HL also influenced various aspects of plant biomass. Biomass of green leaves in the W and HL treatments was almost twice that of the no-HL treatment (Fig. 5). Belowground biomass in the top and bottom layers was significantly lower in W than in the no-HL treatment, with intermediate root biomass in the HL treatment. Root biomass inside the ingrowth cores and the percentage of ingrowth cores colonized by roots did not differ among treatments or core type (OM or soil-only; Table 1). Total aboveground live biomass (green leaves, stolons and base of tillers), dead biomass, and total biomass did not differ significantly among treatments (Fig. 5). Root-to-shoot (green leaf) ratios in the no-HL treatment were significantly higher than in the HL and W treatments (Table 3). Specific leaf area in the W treatment was significantly higher than in the HL and no-HL treatments, and total leaf N content differed among all treatments and was the highest in the W treatment, whereas total root N content did not differ among treatments.

Discussion

Our results show that *Bouteloua dactyloides* performed hydraulic lift, and that HL enhanced organic matter decomposition and aboveground N uptake, especially leaf N uptake, and tended to increase N mineralization, all of which were hindered in plants prevented from performing HL.

There were significantly wetter soil matric potentials in the upper compartments of the HL treatment compared to the dead-plant S12 treatment, which were identical except for the absence of roots in S12. We suggest that the occurrence of hydraulic lift is the only possible explanation for the wetter soil in HL treatment. On average, upper-layer soils of HL treatment were 0.60 ± 0.02 MPa wetter than that of S12 treatment, similar in magnitude to those reported by Aanderud and Richards (2009) and Snyder et al. (2008) for other species performing HL. We found no such differences for the no-HL and S24 treatments, indicating little or no hydraulic lift of water by plants in the no-HL treatment. The greater reduction in soil matric potential over time in the upper soil layer in no-HL and S24

Table 2 Correlations among soil water content (*SW*) at the end of the experiment, mineral nitrogen in ^{15}N-OM-cores (*NH_4-N*, *NO_3-N* and *NH_4:NO_3*), N mineralization (*N-min*) and organic matter decomposition (*%C_{loss}*) in OM-cores, aboveground green biomass, nitrogen content in leaves, ^{15}N content in leaves and percentage of ^{15}N from OM-cores uptaken by leaves

	SW	NH_4-N	NO_3-N	NH_4:NO_3	N-min	C_{loss} (%)
Soil water content, SW (%)						
NH_4-N (μg g^{-1})	0.62***					
NO_3-N (μg g^{-1})	**0.79*** **	0.47***				
NH_4:NO_3	**0.95*** **	**0.75*** **	**0.78*** **			
N-min (μg N g^{-1} $month^{-1}$)	0.62***	–	0.47***	**0.75*** **		
Decomposition (%C_{loss} $month^{-1}$)	0.48***	0.35*	0.58***	0.54***	0.35*	
Aboveground mass (g)	0.25 ns	0.14 ns	0.37*	0.18 ns	0.14 ns	0.03 ns
N_{leaves} (mg g^{-1})	**0.80*** **	0.42**	**0.78*** **	**0.72*** **	0.42**	0.40**
$\delta^{15}N_{leaves}$ (‰)	**0.80*** **	0.52***	0.55***	**0.74*** **	0.52***	0.25 ns
$^{15}N_{uptake}$ (%)	**0.71*** **	0.36*	0.53***	0.59***	0.36*	0.17 ns

Numbers are the R^2 values; asterisks denote significant correlation: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; *ns* non-significant. R^2 values larger than 0.7 are in bold. All significant correlations are positive except for nitrate versus all other variables

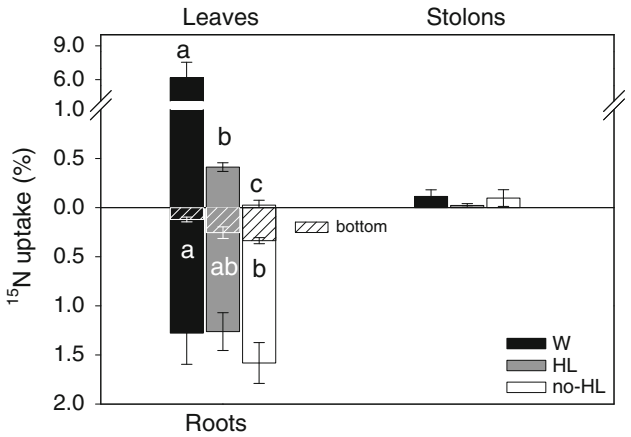

Fig. 4 Percentage of ^{15}N from OM-cores taken up by leaves, stolons, and roots of *Bouteloua dactyloides* subjected to different regimes of water and light (mean ± 1SE; $n = 6$ except 3 for stolons). *Bars* for roots in bottom soil layer (*striped pattern*) are stacked with roots in the upper layer. Bars with different letters denote significant differences at $P < 0.05$ (for leaves and roots in bottom layer). Legend as Fig. 1

treatments may have been promoted by continuous illumination increasing total evaporation (S24) compared to treatments in the 12-h light cycle chamber. Nevertheless, the strong correlation between soil moisture and nutrient processes examined in this study suggests that additional water from HL increased nutrient availability and plant N uptake, as discussed next.

Because nutrients were added as ground litter, we were able to analyze the effect of HL on organic matter decomposition and nutrient mineralization, as well as plant nitrogen uptake. The positive correlation between decomposition rates in the ^{15}N-OM cores and soil moisture, along with higher decomposition rates in the ^{15}N-OM cores in the HL treatment than in the no-HL treatment, indicates that higher soil moisture from HL or watering was a key driver of decomposition and nutrient release in the OM cores. However, significant decomposition even in the drier no-HL treatment highlights the importance of microbial processes in water-limited environments. To our knowledge, only one previous study has analyzed the effect of HL on OM decomposition (Aanderud and Richards 2009). They showed that high-magnitude HL cycles stimulated decomposition of dead roots, possibly by increasing root-driven water fluxes and organic-compound rhizodeposition.

Along with increased OM decomposition, higher soil moisture also stimulated N mineralization, indicating that N mineralization outpaced plant and microbial uptake, immobilization, and nitrification of ammonium as soil moisture increased. We surmise that the lack of significant difference in N-mineralization between the HL and no-HL treatments was due to the higher N assimilation and ^{15}N plant uptake in the HL compared to the no-HL treatment. This idea is supported by the strong positive correlation between final soil moisture, soil NH_4^+ content, and plant ^{15}N uptake. In general, N mineralization is limited by precipitation pulses in dry environments (Yahdjian et al. 2006), and our results indicate that daily moisture supply from HL may enhance soil nitrogen availability from increased OM decomposition and mineralization.

Unlike relatively immobile NH_4^+, NO_3^- is a highly soluble and mobile compound (Miller and Cramer 2005; Raven et al. 1992). This difference likely made soil NO_3^- more available to roots and also more likely to be leached from the root zone (Miller and Cramer 2005). Dawson (1997) also found reduced NO_3^- concentrations in soils around roots performing HL compared to no-HL plants and pointed to the high diffusivity of NO_3^- as a likely

Table 3 Plant growth parameters including root-to-shoot ratio (shoot is considered the biomass of live leaves only), specific leaf area (*SLA*), total *N* concentration in leaves and roots (mean ± 1SE; $n = 6$), $\delta^{15}N$ in leaves, stolons and roots from lower compartment (mean ± 1SE; $n = 3$ for stolons, $n = 6$ for leaves and roots) and overall above- (leaves and stolons) and below-ground plant ^{15}N content (mean ± 1SE; $n = 5$–6)

	W	HL	no-HL	$F_{2,17}$
R:S green	4.81 ± 0.28 a	5.97 ± 0.50 a	11.42 ± 0.54 b	59.60***
SLA (m^{-2} kg−1)	13.55 ± 0.59 a	10.50 ± 0.57 b	9.53 ± 0.13 b	17.08***
N_{leaves} (mg g^{-1} dry mass)	13.63 ± 0.56 a	10.65 ± 0.23 b	7.33 ± 0.73 c	32.71***
N_{roots} (mg g^{-1} dry mass)	4.38 ± 0.25	4.62 ± 0.08	4.93 ± 0.20	2.29 ns
δ^{15}N leaves (‰)	1,982.53 ± 307.81 a	130.16 ± 48.54 b	20.75 ± 7.42 c	37.52***
δ^{15}N stolons (‰)	286.88 ± 125.61	20.99 ± 15.44	11.96 ± 11.44	4.53†
δ^{15}N roots (‰)	211.89 ± 91.99 a	36.38 ± 26.49 b	13.60 ± 2.67 b	11.32***
Above ^{15}N uptake (%)	5.70 ± 1.33 a	0.57 ± 0.15 b	0.10 ± 0.04 c	42.45***
Below ^{15}N uptake (%)	1.92 ± 0.22	1.61 ± 0.16	1.92 ± 022	0.99 ns

Values in rows with different letters indicate significant differences among treatments ($P < 0.05$); asterisks denote significant F values: †$P < 0.07$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, *ns* non-significant. Legend of treatments as Table 1

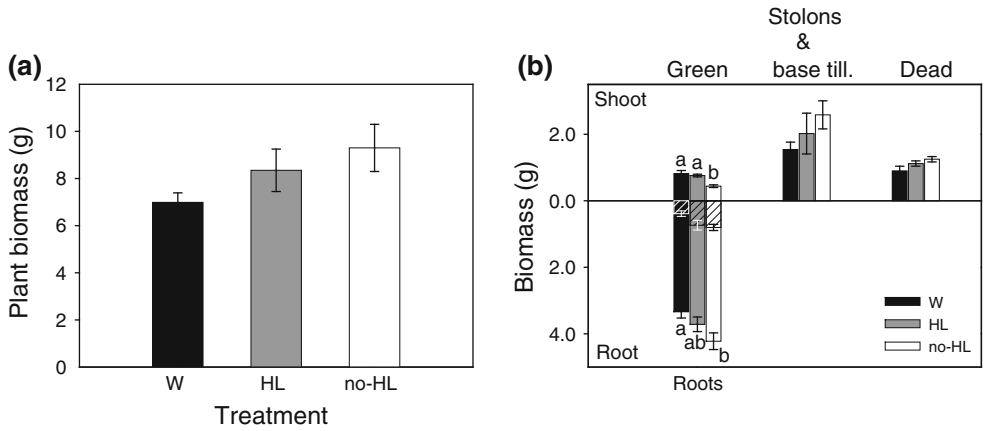

Fig. 5 Total plant biomass (**a**); shoot biomass: green leaves, stolons + base of tillers and dead tissues, root biomass (**b**): roots in bottom soil layer (*striped pattern*) stacked with roots in the upper layer (*solid pattern*; mean ± 1SE; $n = 6$). *Different letters within the grouped bars* denote significant differences within each group at $P < 0.05$, *bars without letters* denote non-significant differences. Legend as in Fig. 1

explanation. Nitrate is the dominant form of N in drier environments and the preferred source for some plants (Schlesinger 1997; Virginia and Jarrell 1983). Low NO_3^- in OM cores of treatments with higher soil moisture (HL and W) could be due to either higher plant uptake or lower nitrification relative to no-HL treatment. However, as nitrification increases with soil moisture in unsaturated conditions (Maag and Vinther 1996; Stark and Firestone 1995), lower NO_3^- levels in HL and W treatments point to higher uptake of NO_3^- rather than low nitrification.

While ^{15}N uptake by belowground tissues was similar across treatments, there was greater aboveground uptake of ^{15}N in the HL and W treatments compared to plants where HL was impaired, indicating that HL mainly affected plant allocation of acquired N to photosynthetic tissues. This effect likely stemmed from enhanced litter decomposition, higher soil mineral N contents in the OM-cores, higher soil water availability and prolonged root activity, as hydraulic redistribution can extend fine root survivorship and function (Bauerle et al. 2008; Rose et al. 2008). Despite the significant differences in ^{15}N uptake among our treatments, some N uptake, OM decomposition, and N mineralization occurred in the no-HL treatment, which indicates that roots in the no-HL treatment were still active. Some desert species have the capacity to take up nutrients from very dry soils (e.g., ∼−5 MPa; Matzner and Richards 1996), and Buffalo grass may be able to extract nutrients even under dry soil conditions (Huang 1999). Previous studies found that HL did not increase plant acquisition of NO_3^- (Snyder et al. 2008) or other nutrients (see Online resource 1 for details; Crabtree et al. 1998; Hawkins et al. 2009; Rose et al. 2008; Wang et al. 2009), while other studies suggested that HL increased plant uptake of mineral N compounds (Dawson 1997; de Kroon et al. 1998; Huang 1999; Leffler et al. 2004). However, all these latter studies added labeled N as liquid pulses, and thus the nutrient could have

been taken up by plants immediately, despite varying soil moisture conditions of the treatments (Austin et al. 2004; Gebauer and Ehleringer 2000; Jackson et al. 1990), potentially confounding the interpretation of the results.

The higher nutrient status of plants from the HL and W treatments compared to the no-HL treatment did not lead to significant gains in biomass but instead resulted in different allocation to above and belowground parts. Larger allocation to aboveground biomass is observed in nutrient-rich conditions (Chapin 1991; Tilman 1988), and the higher green leaf mass that we observed in treatments with higher soil moisture may indicate higher photosynthetic capacity conferred by enhanced plant water and nutrient status. Greater availability of both water and nutrients due to HL may make plants performing HL better competitors for light, as greater nutrient availability is associated with greater leaf area in many grass species (Knight 1973; Knops and Reinhart 2000).

Some limitations of our experimental design merit discussion. The method of applying continuous illumination (CI) to plants at night has been used successfully in many previous HL experiments (Bauerle et al. 2008; Caldwell and Richards 1989; Dawson 1997). In fact, it is the only way to experimentally prevent hydraulic lift from occurring, as other manipulations such as those altering the humidity around the leaves at night (e.g., Snyder et al. 2008) can enhance the amount of water lifted via HL, but cannot suppress HL. However, although the use of CI successfully inhibited HL, it may have caused depletion of soil water due to higher evaporation in the no-HL treatment compared to the HL treatment. In turn, this difference could have increased differences in rates of biogeochemical processes and plant nutrient uptake between plant treatments. Nevertheless, our results clearly show that HL occurred, increasing soil water content in upper layers. Moreover, our measured biogeochemical processes and foliar nutrient uptake were strongly correlated to soil water content, indicating that soil water content positively affected nutrient release and plant uptake. Overall, these results support the idea that hydraulic lift played a significant and positive role in OM decomposition, soil nutrient cycling, and foliar N uptake.

Continuous illumination (CI) can also affect plant physiology and growth, depending on the species and intensity of the light (Velez-Ramírez et al. 2011 and references therein). CI can in some cases induce leaf chlorosis or other disorders (e.g., Ohyama et al. 2005), although we saw no evidence for this. CI reduced the photosynthetic capacity of some boreal conifers but not in others (Equiza et al. 2006). Most authors have found positive effects of CI on seedling mass, pigment content and photosynthetic rates when the PPF was low, as in our study ($\sim$150–500 μmol m^{-2} s^{-1}; e.g., Equiza et al. 2006; Xiao et al. 2007). Lack of differences among treatments in net photosynthetic rates, stomatal conductance, and leaf water potential in our study (data not shown), as well as in total or aboveground biomass, suggest that treatment differences in biomass allocation and physiological status were more a response to soil water and N availability rather than to differences in the light regime.

Overall, we found that nutrients can be mobilized from organic material in dry soil and that plants can subsequently take up mobilized nutrients when small amounts of water are supplied to the root zone via HL. Our experiment was conducted in dry soils, beyond the wilting point of many crop plants ($\Psi_S < -1.5$ MPa), and not surprisingly, the amount of nutrients taken up by HL-enhanced plants was substantially less than that of well-watered control plants. However, HL plants were able to maintain a reasonable degree of physiological activity and growth and higher nutrient status compared to no-HL plants. These results suggest that, while the amount of nutrients taken up in dry soil following HL may be small, it could serve to reduce nutrient deficiency. On a larger scale, results from our study suggest several possible implications of HL on ecosystems that need further study. For example, the fact that HL can enhance nutrient availability and uptake indicates that this mechanism or reverse HL (McCulley et al. 2004) may promote greater nutrient cycling in some systems. Enhanced OM decomposition with HL may also be one mechanism responsible for soil organic carbon losses accompanying afforestation and woody plant invasion of grasslands (Guo and Gifford 2002; Jackson et al. 2002), a vegetation shift resulting in deeper root systems that may promote HL phenomena.

In conclusion, our results show that, by maintaining daily water fluxes and higher overall soil moisture, HL by *Bouteloua dactyloides* enhanced organic matter decomposition, tended to increase N mineralization, and enhanced leaf and overall aboveground N uptake. All these are critical processes for plant nutrient acquisition, which was reduced in plants prevented from performing HL. We also found strong relationships between soil moisture and soil OM decomposition, soil mineral N content, leaf N content, and leaf ^{15}N acquisition. The enhanced water and nutrient conditions apparently improve aboveground plant physiological responses, with altered biomass allocation compared to plants prevented from performing HL. Overall, our results suggest that HL could have positive effects on multiple aspects of plant nutrient dynamics and nutrient turnover.

Acknowledgments We want to thank Todd Smith and the Duke Phytotron staff for help growing the plants and in designing the pots, Tom Rutherford from the Oil-Dri company for kindly providing us the soil. C.A. was supported by a Spanish MEC-Fulbright fellowship. J.H.K. was supported by a U.S. EPA STAR fellowship. T.M.B. was

supported by the Australian Research Council. The U.S. National Science Foundation (DEB 0717191 and IOS 0920355) provided primary support for the experiment.

References

Aanderud ZT, Richards JH (2009) Hydraulic redistribution may stimulate decomposition. Biogeochemistry 95:323–333

Armas C, Padilla FM, Pugnaire FI, Jackson RB (2010) Hydraulic lift and tolerance to salinity of semiarid species: consequences for species interactions. Oecologia 162:11–21

Austin AT et al (2004) Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221–235

Bauerle TL, Richards JH, Smart DR, Eissenstat DM (2008) Importance of internal hydraulic redistribution for prolonging the lifespan of roots in dry soil. Plant Cell Environ 31:177–186

Bleby TM, McElrone AJ, Jackson RB (2010) Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. Plant Cell Environ 33:2132–2148

Brown RW (1970) Measurement of water potential with thermocouple psychorometers: construction and application. US Forestry Service Research Paper INT-293

Burgess SSO, Bleby TM (2006) Redistribution of soil water by lateral roots mediated by stem tissues. J Exp Bot 57:3283–3291

Caldwell MM, Manwaring JH (1994) Hydraulic lift and soil nutrient heterogeneity. Isr J Plant Sci 42:321–330

Caldwell MM, Richards JH (1989) Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. Oecologia 79:1–5

Caldwell MM, Dawson TE, Richards JH (1998) Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113:151–161

Chapin FS (1991) Effects of multiple environmental stresses on nutrient availability and use. In: Mooney HA, Winner WE, Pell EJ, Chu E (eds) Response of plants to multiple stresses. Academic, San Diego, pp 67–88

Crabtree WL, Robson AD, Ritchie GSP (1998) Drying of surface soil decreased *Lupinus angustifolius* root length and manganese uptake in a split-root experiment. Aust J Agric Res 49: 1119–1123

Dawson TE (1993) Hydraulic lift and the water use by plants: implications for water balance, perfomance and plant–plant interactions. Oecologia 95:565–574

Dawson TE (1997) Water loss from tree influences soil water nutrient status and plant performance. In: Flores EH, Lynch JP, Eissenstat D (eds) Radical biology: advances and perspectives on the function of plant roots, vol 18. American Society of Plant Physiologists, Rockville, pp 235–250

de Kroon H, van der Zalm E, van Rheenen JWA, van Dijk A, Kreulen R (1998) The interaction between water and nitrogen translocation in a rhizomatous sedge (*Carex flacca*). Oecologia 116:38–49

Equiza MA, Day ME, Jagels R (2006) Physiological responses of three deciduous conifers (*Metasequoia glyptostroboides*, *Taxodium distichum* and *Larix laricina*) to continuous light: adaptive implications for the early tertiary polar summer. Tree Physiol 26:353–364

Gebauer RLE, Ehleringer JR (2000) Water and nitrogen uptake patterns following moisture pulses in a cold desert community. Ecology 81:1415–1424

Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: a meta analysis. Glob Change Biol 8:345–360

Hawkins HJ, Hettasch H, West A, Cramer MD (2009) Hydraulic redistribution by Protea 'Sylvia' (Proteaceae) facilitates soil water replenishment and water acquisition by an understorey grass and shrub. Funct Plant Biol 36:752–760

Huang B (1999) Water relations and root activities of *Buchloe dactyloides* and *Zoysia japonica* in response to localized soil drying. Plant Soil 208:179–186

Jackson RB, Manwaring JH, Caldwell MM (1990) Rapid physiological adjustment of roots to localized soil enrichment. Nature 344:58–60

Jackson RB, Sperry JS, Dawson TE (2000) Root water uptake and transport: using physiological processes in global predictions. Trends Plant Sci 5:482–488

Jackson RB, Banner JL, Jobbágy EG, Pockman WT, Wall DH (2002) Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418:623–626

Jobbágy EG, Jackson RB (2004) The uplift of soil nutrients by plants: biogeochemical consequences across scales. Ecology 85:2380–2389

Knight DH (1973) Leaf area dynamics of a shortgrass prairie in Colorado. Ecology 54:891–896

Knops JMH, Reinhart KO (2000) Specific leaf area along a nitrogen fertilization gradient. Am Midl Nat 144:265–272

Lee JE, Oliveira RS, Dawson TE, Fung I (2005) Root functioning modifies seasonal climate. Proc Natl Acad Sci USA 102:17576–17581

Leffler AJ, Ivans CY, Ryel RJ, Caldwell MM (2004) Gas exchange and growth responses of the desert shrubs *Artemisia tridentata* and *Chrysothamnus nauseosus* to shallow- vs. deep-soil water in a glasshouse experiment. Environ Exp Bot 51:9–19

Liste H, White JC (2008) Plant hydraulic lift of soil water-implications for crop production and land restoration. Plant Soil 313:1–17

Maag M, Vinther FP (1996) Nitrous oxide emission by nitrification and denitrification in different soil types and at different soil moisture contents and temperatures. Appl Soil Ecol 4:5–14

Matzner SL, Richards JH (1996) Sagebrush (*Artemisia tridentata* Nutt) roots maintain nutrient uptake capacity under water stress. J Exp Bot 47:1045–1056

McCulley RL, Jobbagy EG, Pockman WT, Jackson RB (2004) Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. Oecologia 141:620–628

Miller AJ, Cramer MD (2005) Root nitrogen acquisition and assimilation. Plant Soil 274:1–36

Nambiar EKS (1976) Uptake of Zn65 from dry soil by plants. Plant Soil 44:267–271

Ohyama K, Omura Y, Kozai T (2005) Effects of air temperature regimes on physiological disorders and floral development of tomato seedlings grown under continuous light. Hortscience 40:1304–1306

Prieto I, Padilla FM, Armas C, Pugnaire FI (2011) The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. Perspect Plant Ecol Evol Syst (in press)

Querejeta JI, Egerton-Warburton LM, Allen MF (2003) Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. Oecologia 134:55–64

Raven JA, Wollenweber B, Handley LL (1992) A comparison of ammonium and nitrate as nitrogen sources for photolithotrophs. New Phytol 121:19–32

Redmann RE (1978) Plant and soil water potentials following fire in a northern mixed grassland. J Range Manag 31:443–445

Rice CW (2006) Organic matter and nutrient dynamics. In: Lal R (ed) Encyclopedia of soil science, vol II. Taylor and Francis, New York, pp 1181–1183

Richards JH, Caldwell MM (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73:486–489

Rose TJ, Rengel Z, Ma Q, Bowden JW (2008) Hydraulic lift by canola plants aids P and K uptake from dry topsoil. Aust J Agric Res 59:38–45

Scanlon BR, Reedy RC, Stonestrom DA, Prudic DE, Dennehy KF (2005) Impact of land use and land cover change on groundwater recharge and quality in the southwestern US. Glob Change Biol 11:1577–1593

Schlesinger WH (1997) Biogeochemistry: an analysis of global change. Academic, San Diego

Scott RL, Cable WL, Hultine KR (2008) The ecohydrologic significance of hydraulic redistribution in a semiarid savanna. Water Resour Res 44:W02440

Smart DR, Carlisle E, Goebel M, Nunez BA (2005) Transverse hydraulic redistribution by a grapevine. Plant Cell Environ 28: 157–166

Snyder KA, James JJ, Richards JH, Donovan LA (2008) Does hydraulic lift or nighttime transpiration facilitate nitrogen acquisition? Plant Soil 356:159–166

Stark JM, Firestone MK (1995) Mechanisms for soil moisture effects on activity of nitrifying bacteria. Appl Environ Microbiol 61: 218–221

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton

Valenzuela-Estrada LR, Richards JH, Díaz A, Eissenstat DM (2009) Patterns of nocturnal rehydration in root tissues of *Vaccinium corymbosum* L. under severe drought conditions. J Exp Bot 60:1241–1247

Velez-Ramírez AI, van Ieperen W, Vreugdenhil D, Millenaar FF (2011) Plants under continuous light. Trends Plant Sci 16:310–318

Virginia RA, Jarrell WM (1983) Soil properties in a mesquite-dominated Sonoran Desert ecosystem. Soil Sci Soc Am J 47:138–144

Wang X, Tang C, Guppy CN, Sale WG (2009) The role of hydraulic lift and subsoil P placement in P uptake of cotton (*Gossypium hirsutum* L.). Plant Soil 325:263–275

Warren JM, Brooks R, Meinzer FC, Eberhart JL (2008) Hydraulic redistribution of water from *Pinus ponderosa* trees to seedlings: evidence for an ectomycorrhizal pathway. New Phytol 178:382–394

Weaver JE (1958) Summary and interpretation of underground development in natural grassland communities. Ecol Monogr 28:55–78

Xiao YL, Zhang YT, Dang K, Wang DS (2007) Effects of continuous 24 h photoperiod on growth and photosynthesis in *Platycodon grandiflorum* (Jacq.) A. DC. plants. Propag Ornam Plants 7:216–218

Yahdjian L, Sala OE, Austin AT (2006) Differential controls of water input on litter decomposition and nitrogen dynamics in the Patagonian steppe. Ecosystems 9:128–141