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HYDRAULIC LIFT AND SOIL NUTRIENT HETEROGENEITY

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ABSTRACT

Water released at night from roots into upper portions of the soil profile in the process of hydraulic lift may contribute to reducing spatial soil nutrient heterogeneity. A manipulative field experiment was conducted in a semiarid shrub stand to determine if circumvention of hydraulic lift, by nighttime illumination of the shrub canopy, would result in greater soil nutrient heterogeneity than if the hydraulic lift process was allowed to operate. Nutrient-enriched patches were superimposed on the existing soil heterogeneity and after 40 days, the patches and interspaces were sampled for ions of different mobility and for root mass. There was no indication under these conditions that hydraulic lift was contributing to smoothing spatial nutrient heterogeneity.

INTRODUCTION

Hydraulic lift involves nighttime movement of water into roots in relatively moist portions of the soil profile and then efflux of this water from roots in drier regions of the profile (Richards and Caldwell, 1987). Since soils usually dry from the surface downward, both due to evaporation and root system extraction, deeper layers of the profile are usually more moist and, thus, the source of water for hydraulic lift (Caldwell et al., 1991). There are several potentially important implications of hydraulic lift for individual plants, such as facilitating the effectiveness of water extraction from the soil when levels of evaporation are high (Caldwell and Richards, 1989) and buffering the seasonal course of soil water depletion in the rooting zone against day-to-day fluctuations in evapotranspiration (Williams et al., 1993). Under prolonged periods without precipitation, release of moisture by roots in upper soil layers could contribute to maintenance of fine roots and mycorrhizae and possibly to nutrient uptake from relatively dry soil (Nambiar, 1976, 1977).

There are also implications of hydraulic lift at the community and ecosystem levels. For example, at the community level, Dawson (1993) has shown that water released by hydraulic lift of a deep-rooted tree can provide as much as 60% of the water supply to proximate, shallow-rooted herbaceous plants during prolonged dry periods. Thus, neighboring plants with overlapping root systems may not only experience competition for below-ground resources but also facilitation of resource availability under some

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conditions. Ecosystem-level processes such as nutrient cycling and availability may also be affected by hydraulic lift if soil moisture distribution is altered during periods of negligible precipitation. One aspect of nutrient availability is the spatial heterogeneity of nutrient distribution on the scale of centimeters to decimeters. Spatial variability at this scale can be as great as on the scale of several meters (Jackson and Caldwell, 1993a,b). Patchiness in soil nutrient distribution at the centimeter–decimeter scale has been shown to influence root distributions, physiological properties, and competition between plants for soil resources (Caldwell, 1994; Grime, 1994).

Without hydraulic lift, this spatial heterogeneity could be more pronounced. There are several ways in which efflux of water from fine roots in upper drier soil layers may contribute to some smoothing of nutrient heterogeneity. Physical processes such as nutrient diffusion will be promoted at greater soil moisture content. Biological processes such as microbial and root activity will also be facilitated, which in turn can contribute to some smoothing of soil heterogeneity. For example, if higher-plant roots have a tendency to grow and proliferate in nutrient-rich microsites, as shown in many species (Robinson, 1994), greater soil moisture should facilitate this behavior. This, coupled with greater diffusion and root physiological uptake capacity (Caldwell, 1994), may contribute to preferential utilization of the rich microsites and thereby cause some leveling of the variability. Alternatively, enhanced microbial activity resulting from moisture delivered by hydraulic lift could lead to increased heterogeneity for some nutrients under certain circumstances (Stark, 1994). In this paper, we describe experiments designed to test the possible influence of hydraulic lift on soil nutrient spatial variability.

Testing implications of hydraulic lift for community and ecosystem-level processes under field conditions is difficult and not entirely free of confounding effects of the treatment. To prevent or minimize hydraulic lift, nighttime illumination has been used in manipulative experiments. This forces stomates to open at night allowing the acquired water to flow in the normal soil–plant–atmosphere stream instead of into the drier soil layers, since the dominating water potential gradient is in the direction of the atmosphere. This method works well in circumventing hydraulic lift (Caldwell and Richards, 1989), and since temperatures are cooler at night, less water is transpired than during the day. Although transpiration continued at night in these earlier experiments, total 24-h transpiration was about the same as without nighttime lighting because daytime transpiration was greatly curtailed in the absence of hydraulic lift. Thus, the diel pattern of water loss in transpiration was changed, but the overall rate was about the same. Unlike the earlier experiments, to test questions involving nutrient heterogeneity it becomes necessary to suspend hydraulic lift over at least several weeks. This may well alter many physiological processes of the higher plants involved and, thus, is an unavoidable artifact in such experiments. Nevertheless, the experiment reported here primarily involved soil nutrient heterogeneity, rather than measures of plant performance *per se*.

Spatial heterogeneity occurs at several spatial scales (Stark, 1994). We chose a centimeter–decimeter scale as appropriate to test the influence of hydraulic lift on nutrient heterogeneity. Considerable spatial variability has been demonstrated in this type of vegetation at this scale (Jackson and Caldwell, 1993a,b). As mentioned above, it is a

relevant scale for plant and competition processes, and the technical constraints of this type of experiment could still be accommodated. We superimposed on the extant spatial variability a strong imprint of nutrient patches for these tests. This provided a much more tractable design than to simply assess the existing heterogeneity. Interspaces were sampled between the nutrient patches to establish a background and to detect if hydraulic lift was effecting some mixing of nutrients between patches and interspaces. For the patches, three different ions were employed that vary several orders of magnitude in diffusivity: $\text{NO}_3^- > \text{K}^+ \gg \text{HPO}_4^{2-}$. Water released from roots by hydraulic lift in relatively dry surface soil should have its greatest effect on ions of higher diffusivity. The range of diffusivities of NO_3^- are somewhat greater than those of K^+ , but both are orders of magnitude greater than HPO_4^{2-} . In the calcareous soils where our experiment was conducted, much of the HPO_4^{2-} would be bound and further slow the potential for movement (Barber, 1974).

METHODS AND MATERIALS

The experiments were conducted in field plots near Logan, Utah ($41^\circ 45' \text{N}$, $111^\circ 48' \text{W}$, 1460 m elevation) in the summer of 1994. The plots had been established in 1978 with small transplants of a shrub, *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle intermixed with perennial tussock grasses in evenly spaced matrices (0.5 m between individuals). The intervening tussock grasses had been removed in the course of earlier experiments about 10 years before the current experiment. Therefore, the plots consisted of only *Artemisia* shrubs with approximate spacings of one meter. The soils are rocky Mollisols (Typic Haploxerolls) which were formed from alluvial material (Southard et al., 1978). Further site details are in Caldwell et al. (1981).

Twelve grids of nutrient-enriched microsites (patches) were installed on July 15, 1994. Each grid consisted of a 4×4 array of patches with 10-cm spacing between patches. These were all at a depth of 20. The dimensions and depth of the array were chosen according to several criteria. The grids needed to be small both to fit between the shrubs and to minimize the distance between individual patches, yet large enough to have distinct interspaces between the patches that could be sampled. The patches themselves needed to be without barriers. Thus, when the liquid nutrient solution was injected some migration from the site of injection occurred. Even with a small quantity of injected solution (5 ml), the resulting patch diameter was approximately 4 cm. The depth of patches was selected to be in a zone of high root density in the upper layers of the profile. At 20 cm, root density is high (Caldwell and Richards, 1986; Richards and Caldwell, 1987). At depths above about 10 cm, root density decreases and the soils can be particularly dry. The technical difficulties in installing patches, and locating and harvesting soil samples from the appropriate microsites precluded having the patch grids at depths greater than 20 cm.

The nutrient patches were installed in each grid by first forcing a series of 6-mm-diameter steel rods into the soil to the desired 20-cm depth. During this procedure, the rods were aligned with a positioning jig to ensure that the holes were both parallel to one another and perpendicular to the soil surface. After the holes were made and the steel rods

extracted, 19-cm-long plastic drinking straws were inserted into each hole so that the nutrient solution would not be absorbed at shallower depths in the soil. Each patch received 5 ml of nutrient solution (1 M KNO_3 , 1 M H_3PO_4). After the solution was absorbed, each straw was filled with soil from the hole and left in position. This enabled more accurate location and removal of the micropatches at the end of the experiment.

The 12 grids were interspersed in interspaces between *Artemisia* shrubs. The shrubs around six of the grids (hydraulic lift circumvention treatment) were given nighttime lighting from 1500-W metal halide lamps suspended from an aluminum framework above the shrub canopy. Depending on location, this provided 200–700 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (400–700 nm) at the top of the canopy. In earlier work in the same location with *Artemisia*, the procedure worked well in causing stomates to remain open at night and to, therefore, circumvent hydraulic lift (Caldwell and Richards, 1989). In preliminary work for the present experiment conducted in 1992 and 1993, nighttime lighting was also shown to work well for periods of several weeks in circumventing hydraulic lift (based on diel patterns of soil moisture potential). The six control grids did not have nighttime illumination. The treatment period lasted 40 ± 1 day (depending on when individual grids were harvested).

The experiment was intentionally conducted during a time of year when there is little precipitation that penetrates more than a few mm into the soil. Thus, during the long drying cycle of the summer, precipitation did not dilute or cause mass movement of the nutrients in the patches. Also, there was no problem with rain water infiltrating preferentially down the sides of the straws used to install and mark the nutrient patches. During 1994, precipitation was 30% less than the long-term average of 494 mm at this site.

Soil samples were collected from each nutrient patch and from interspace positions located midway between 4 equidistant nutrient patches (for the 16 nutrient patches in a grid there were 9 interspace positions sampled). The sample extraction required three days; two control and two treatment grids were collected each day. For each sample, a 2.8-cm-diameter steel tube was driven into the soil, using the straw as a guide, and the top 20 cm of soil was discarded. The sample consisted of soil in the core depth increment of 20–25 cm. This was immediately sieved (2-mm mesh), an aliquot of this was added to a preweighed centrifuge tube containing 2 M KCl, and the remainder of the soil sample put in another preweighed tube. Root material from the sample was placed in a glass vial for drying and weighing.

The 2 M KCl samples were extracted, filtered, and frozen on the day of collection; the remaining samples were air dried at 70 °C for 48 h. The KCl-extractable NO_3^- was determined with a LaChat autoanalyzer (USEPA, 1983). Moisture content was determined gravimetrically and NO_3^- analyses adjusted to a basis of soil dry mass. The NaHCO_3 -extractable HPO_4^{2-} and K^+ were determined by colorimetry (Murphy and Riley, 1962) and flame emission spectrophotometry (Hamm et al., 1970), respectively. Root mass was estimated by dry ashing the samples at 550 °C for 12 h and subtracting ash mass from total root dry mass.

In preliminary work in 1992 and 1993, several methods of installing patches and accurately retrieving soil samples from the patches and interspaces were tested. As

explained above, the dimensions of the grid selected constituted a reasonable compromise in order to have small distances between nutrient patch and interspace samples and yet to cleanly extract the desired samples without inadvertent mixing. Since the HPO_4^{2-} ion is very immobile in these calcareous soils, it could be used as an indication of inadvertent mixing of the soil samples from nutrient patches and interspaces. Unusually high interspace concentrations of soil HPO_4^{2-} (> 25 ppm based on these samples and previous sampling in this area) were an indication of inadvertent mixing and were removed from the analysis. This constituted less than 4% of the total interspace samples and about 1% of the total samples. Based on this indicator, it was apparent that most of the samples were cleanly extracted.

Data were analyzed by a one-way analysis of variance for the variables: NO_3^- , K^+ , and HPO_4^{2-} ion concentrations, root mass, water content at end of the experiment, and for each of these variables, a parameter Q, indicating the relative difference of nutrient patches and interspace concentrations,

$$Q = \frac{x - y}{x}$$

where x is the nutrient patch parameter and y is the interspace parameter. For each parameter, individual core samples within each grid were averaged for the nutrient-patch and interspace samples. These were used in the analysis of variance with nighttime lighting as the treatment; therefore, $n = 6$.

RESULTS AND DISCUSSION

The nutrient patches superimposed on the natural soil heterogeneity clearly left a recognizable imprint of the three ions selected for the study. A depiction of one control grid (Fig. 1) indicates the positions of the nutrient patch and interspace samples, the concentrations of the three ions, and the root mass from each sample. Based on the observed outward migration of nutrient solution from test patches, the approximate perimeter of the nutrient patches after solution absorption in the soil is also indicated. The distance between this perimeter and the edge of the sample cores of the interspace samples was 3.5 cm.

The average nutrient concentrations for patch and interspace samples are given in Table 1 for the control and treatment grids along with a parameter, Q. One-way analysis of variance did not indicate significant treatment differences for any of the ion concentrations or root mass in either the nutrient patches or the interspaces. The only significant treatment difference was in soil water content between treatments. However, the mean differences between treatments were extremely small (< 0.25%). The Q value was not significant for any of the parameters.

Hydraulic lift, although known earlier as a possibility from laboratory experiments (e.g., van Bavel and Baker, 1985), was later shown in the field to result in considerable water movement in soils (Richards and Caldwell, 1987). During one night, water transfer from lower to upper soil layers was estimated to be on the order of one-third to one-half

Fig. 1. A scale diagram of one control grid indicating the positions of the nutrient patch and interspace soil samples (heavy rings indicating diameter of coring device — 2.8 cm diameter). The approximate diameter of the wetting front associated with installing the nutrient patches is indicated by thin-line circles. Concentrations of NO_3^- , K^+ , and HPO_4^{2-} ions and root mass in the cores are also given.

Table 1
Nutrient ion concentrations, root mass, and water content in nutrient patches and interspaces and Q statistic (mean of 6 grids per treatment and standard error)

Parameter	Control (with hydraulic lift)		Q	Treatment (without hydraulic lift)		Q
	Nutrient patches	Interspaces		Nutrient patches	Interspaces	
NO ₃ ⁻ (ppm)	4.69 ± 0.23	0.99 ± 0.12	0.786 ± 0.026	4.57 ± 0.23	1.26 ± 0.15	0.725 ± 0.043
K ⁺ (ppm)	338.77 ± 13.46	123.9 ± 5.12	0.618 ± 0.048	334.74 ± 13.99	130.52 ± 3.96	0.600 ± 0.034
HPO ₄ ²⁻ (ppm)	104.92 ± 7.66	3.89 ± 0.21	0.959 ± 0.006	98.97 ± 6.59	4.32 ± 0.30	0.953 ± 0.006
Root mass (mg)	36 ± 10	27.5 ± 1.0	-0.063 ± 0.2319	28.0 ± 1.0	50.6 ± 20	-2.1939 ± 2.433
Water content (%)	3.04 ± 0.05	3.00 ± 0.08	0.012 ± 0.02	2.82 ± 0.06	2.75 ± 0.07	0.019 ± 0.03

of the daily evapotranspiration in this *Artemisia* shrub stand (Richards and Caldwell, 1987; Caldwell and Richards, 1989). Thus, the potential for considerable influence on soil processes during long drying cycles exists. Depending on weather and general soil moisture conditions, the nighttime increase of soil water potential, Ψ_s , could range from 0.2 MPa to as much as 1 MPa. Even though hydraulic lift brings about diel increases of Ψ_s , this is superimposed on a general decline in Ψ_s during the course of long drying cycles (Fig. 2).

Our current experiment did not show that the intentionally created soil nutrient heterogeneity was any different in areas where shrubs were treated to circumvent hydraulic lift than in areas where hydraulic lift was allowed to proceed naturally. There may be many reasons for the lack of apparent effect, including general soil moisture that, despite nighttime increases due to hydraulic lift, was insufficient to allow microbial, plant, and physical processes to operate in leveling the nutrient heterogeneity. At the end of the experiment, soils were very dry at the 20-cm sampling depth (Table 1), and this may have overwhelmed any potential effect of the nighttime increases of Ψ_s . If anything, there was slightly less moisture at the end of the experiment in the plots with nighttime lighting (Table 1). This difference, though statistically significant, was very small (<0.25%) and most likely not of much biological significance.

Fig. 2. The course of soil moisture potential, Ψ_s , at several depths below a monoculture of *Artemisia tridentata* near the study plots. Diel Ψ_s fluctuations are superimposed on a gradual decrease in Ψ_s . Below 120 cm, there are no diel fluctuations apparent. Thus, hydraulic lift is delivering moisture at night at depths as great as 80 cm. Delivery at depths of even 170 cm has been measured (Williams et al., 1993).

The expectation was that if hydraulic lift effected a smoothing of spatial nutrient heterogeneity largely through physical processes such as increased diffusion, HPO_4^{2-} would be little affected, K^+ would be intermediate, and NO_3^- would be most influenced. There was no tendency for such a ranking in the data since Q values for all three ions did not show treatment differences.

Nutrient-enriched soil microsites often elicit an increase in local root growth and proliferation; however, most of the research has been conducted in laboratory and greenhouse conditions (Robinson, 1994). Root proliferation of *Artemisia* has been demonstrated under field conditions (Caldwell et al., 1991 and unpublished data). However, the presence and degree of proliferation in these studies was dependent on several factors, such as the species of neighboring plant sharing the nutrient patch. Thus, the consistency of proliferation in many laboratory and field experiments should not necessarily be expected under field conditions. In the present study, there was no indication of proliferation in nutrient patches (Table 1), although the root mass variability was quite high. Another common response of roots to enriched soil microsites is an increase in physiological root uptake capacity. This has also been demonstrated under field conditions for *Artemisia* (Jackson et al., 1990). This was not measured in the present study; however, there was no indication that roots were effectively lowering the soil nutrient patch ion concentrations.

An experiment even remotely related to this one has never been undertaken, to the best of our knowledge. Manipulative field experiments at the community and ecosystem level are usually difficult and costly (Gurevitch and Collins, 1994). A lack of effect under the conditions of this experiment should not be taken as a suggestion not to pursue these and related questions concerning the implications of hydraulic lift. The significance of hydraulic lift for buffering and storage of water, facilitation of water flux, and water parasitism have been shown (Caldwell and Richards, 1989; Dawson, 1993; Williams et al., 1993). However, the indirect consequences of hydraulic lift for nutrient procurement by plant roots, maintenance of fine roots and mycorrhizae, effects on soil microbial communities, smoothing spatial heterogeneity, and dampening temporal changes in nutrient availability are of potential importance. These phenomena are also difficult to probe experimentally, but worth the challenge.

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REFERENCES

- Barber, S.A. 1974. Soil nutrient bioavailability. A mechanistic approach. Wiley, New York.
Caldwell, M.M. 1994. Exploiting nutrients in fertile soil microsites. In: Caldwell, M.M. and Pearcy, R.

- R.W., eds. Exploitation of environmental heterogeneity by plants: ecophysiological processes above and below ground. Academic Press, San Diego, pp. 325–347.
- Caldwell, M.M. and Richards, J.H. 1986. Competing root systems: morphology and models of absorption. In: Givnish, T., ed. On the economy of plant form and function. Cambridge University Press, Cambridge, pp. 251–273.
- Caldwell, M.M. and Richards, J.H. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* 79:1–5.
- Caldwell, M.M., Richards, J.H., Johnson, D.A., Nowak, R.S., and Dzurec, R.S. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50:14–24.
- Caldwell, M.M., Richards, J.H., and Beyschlag, W. 1991. Hydraulic lift: Ecological implications of water efflux from roots. In: Atkinson, D., ed. Plant root growth: An ecological perspective. Blackwell, Oxford, pp. 423–436.
- Dawson, T.E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant–plant interactions. *Oecologia* 95:565–574.
- Grime, J.P. 1994. The role of plasticity in exploiting environmental heterogeneity. In: Caldwell, M.M. and Percy, R.W., eds. Exploitation of environmental heterogeneity by plants: ecophysiological processes above and below ground. Academic Press, San Diego, pp. 1–19.
- Gurevitch, J. and Collins, S.L. 1994. Experimental manipulation of natural plant communities. *Trends Ecol. Evol.* 9:94–98.
- Hamm, J.W., Radford, F.G., and Halstead, E.H. 1970. The simultaneous determination of nitrogen, phosphorus and potassium in sodium bicarbonate extracts of soils. *Adv. Auto. Anal.* 2:65–69.
- Jackson, R.B. and Caldwell, M.M. 1993a. The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology* 74:612–614.
- Jackson, R.B. and Caldwell, M.M. 1993b. Geostatistical patterns of soil heterogeneity around individual perennial plants. *J. Ecol.* 81:683–692.
- Jackson, R.B., Manwaring, J.H., and Caldwell, M.M. 1990. Rapid physiological adjustment of roots to localized soil enrichment. *Nature* 344:58–60.
- Murphy, J. and Riley, J.P. 1962. A modified single solution method for the determination of phosphates in natural waters. *Anal. Chem. Acta* 27:31–36.
- Nambiar, E.K.S. 1976. Uptake of Zn^{65} from dry soil by plants. *Plant Soil* 44:267–271.
- Nambiar, E.K.S. 1977. The effects of water content of the topsoil on micronutrient availability and uptake in a siliceous sandy soil. *Plant Soil* 46:175–183.
- Richards, J.H. and Caldwell, M.M. 1987. Hydraulic lift: Substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73:486–489.
- Robinson, D. 1994. The responses of plants to non-uniform supplies of nutrients. *New Phytol.* 127:635–674.
- Southard, A., Wilson, L., and Erickson, A. 1978. Chemical and physical properties of the soils of the Cache Valley area and eastern portion of Box Elder County, Utah. *Utah Agric. Exp. Stn. Res. Rep.*, 31.
- Stark, J.M. 1994. Causes of soil nutrient heterogeneity at different scales. In: Caldwell, M.M. and Percy, R.W., eds. Exploitation of environmental heterogeneity by plants. Academic Press, San Diego, pp. 255–284.
- U.S. EPA. 1983. Methods for chemical analysis of waters and wastes. EPA– 600/4–79–020.
- van Bavel, C.H.M. and Baker, J.M. 1985. Water transfer by plant roots from wet to dry soil. *Naturwissenschaften* 72:606–607.
- Williams, K., Caldwell, M.M., and Richards, J.H. 1993. The influence of shade and clouds on soil water potential: the buffered behavior of hydraulic lift. *Plant Soil* 157:83–95.