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E.-D. Schulze · M.M. Caldwell · J. Canadell
H.A. Mooney · R.B. Jackson · D. Parson · R. Scholes
O.E. Sala · P. Trimborn

Downward flux of water through roots (i.e. inverse hydraulic lift) in dry Kalahari sands

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Abstract Downward transport of water in roots, in the following termed "inverse hydraulic lift," has previously been shown with heat flux techniques. But water flow into deeper soil layers was demonstrated in this study for the first time when investigating several perennial grass species of the Kalahari Desert under field conditions. Deuterium labelling was used to show that water acquired by roots from moist sand in the upper profile was transported through the root system to roots deeper in the profile and released into the dry sand at these depths. Inverse hydraulic lift may serve as an important mechanism to facilitate root growth through the dry soil layers underlaying the upper profile where precipitation penetrates. This may allow roots to reach deep sources of moisture in water-limited ecosystems such as the Kalahari Desert.

Key words Water transport · Grass roots · Hydraulic lift · Deserts

E.-D. Schulze (✉)
Max-Planck-Institut for Biogeochemistry, PO Box 100164,
D-07401 Jena, Germany

M.M. Caldwell
Ecology Center, Utah State University,
Logan, UT 84322-5230, USA

J. Canadell · H.A. Mooney
Department of Biological Sciences, Stanford University,
Stanford, CA 94305, USA

R.B. Jackson
Department of Botany, University of Texas,
Austin, TX 78713, USA

D. Parson · R. Scholes
CSIRO Division of Forest Science and Technology,
P Box 395,
Pretoria, South Africa

O.E. Sala
Department of Ecology, University of Buenos Aires,
Av. San Martin 4453,
Buenos Aires 1417, Argentina

P. Trimborn
Institut für Hydrologie, GSF Neuherberg,
Ingolstädter Landstrasse 1,
D-81377 München, Germany

Introduction

A global survey of maximum recorded rooting depths in various ecosystems shows the largest values in deserts and tropical grasslands and savannas (Canadell et al. 1996). In the Kalahari Desert, well drillers must bore to great depths in very dry sand to reach water, and observant drillers reported some of the deepest roots thus far recorded in the world at 68 m (Jennings 1974). In the Kalahari sands, the annual precipitation of less than 300 mm can only penetrate a couple of meters at most. Below this wetting front, roots must, therefore, grow in very dry sand for tens of meters before they can reach deep geologic water (Jennings 1974). A potential mechanism that would facilitate this growth in very dry sand is water transfer through root systems from upper soil layers of greater moisture following precipitation to deeper, drier layers in response to the water potential gradient. The transfer of water from wetter to drier regions of the soil using the root system as a conduit has been termed hydraulic lift (Richards and Caldwell 1987). The term derives from water flow in the liquid phase in an upward direction since the soil water potentials are often more negative in the upper layers of many soil profiles. During drying cycles, soils tend to dry from the surface downward due to greater rooting densities in the upper profile and direct evaporation from the surface.

We hypothesized that with an inverted water potential gradient in the soil profile, the same process should move water from upper to lower sand layers, which would be a downward transport of water which we term "inverse hydraulic lift." This water flux through the roots and efflux into the rhizosphere could facilitate root growth. Over 60 years ago, Breazeale and Crider (1934) speculated that water transfer through roots to growing root tips might assist root growth of desert plants in dry soil in Arizona. Their laboratory experiments also demonstrated this potential. McCully (1995) observed in field-grown agricultural crops, an exudation of water by roots into the root cap mucilage. However, in this study, the transport of water into dry soil was not studied.

We tested the potential for inverse hydraulic lift of three grass species growing in the Kalahari Desert, using deuterium labelling during a field campaign in the year 1996. While the grass roots do not reach the impressive depths mentioned above for woody plants, they can reach a depth of at least 5 m (Canadell et al. 1996) and the principle should apply if the deeper grass roots are in dry sand.

Materials and methods

The sand dune site of this field study was located in northwest South Africa (27°28′S, 20°45′E). The vegetation is dominated by a mixture of woody shrubs and small trees (*Acacia haematoxylon* and *A. erioloba*) and perennial tussock grasses. Three tussock grass species were chosen for this study, *Stipagrostis amabilis*, *S. obtusa*, and *Centropodium glauca*, since it was not feasible to reach depths of abundant fine roots for the woody *Acacia* species.

In March 1996, near the end of the growing season when sands were very dry, we labelled the plants by a surface irrigation with 3–5 l water (corresponding to 25–30 mm precipitation). This irrigation water contained a fairly concentrated deuterium label (100 ml 99.9% D_2O). One to 3 days following the irrigation and labelling, samples of fine roots and sand surrounding these roots were collected well below the wetting front and compared with the natural depth profile of deuterium as a control. A few parallel root and sand samples were also collected in the wetted zone. The samples were sealed in vials. Subsequently, water from the samples was vacuum extracted and the isotope ratios measured by mass spectrometry at the GSF-Forschungszentrum für Umwelt und Gesundheit (Neuherberg, Germany). Stem water potentials were measured with the pressure bomb technique before and after the irrigation.

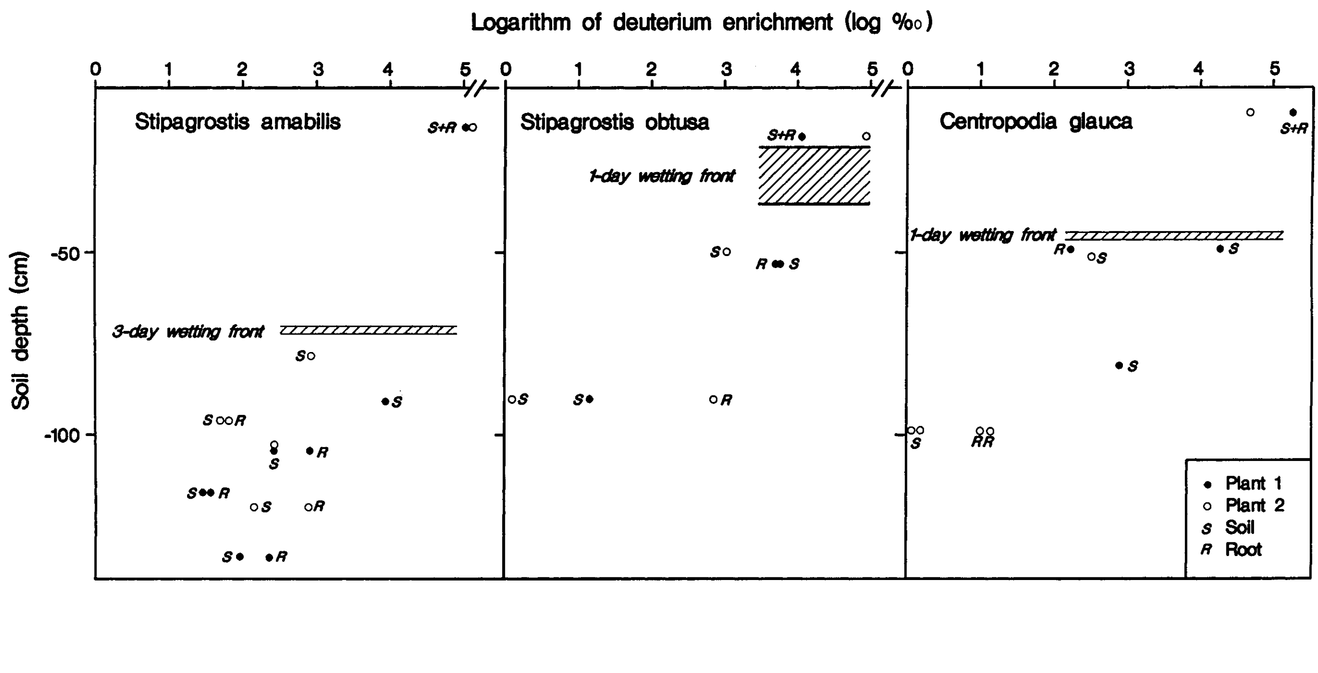
Results

Before the irrigation, the grass stem water potentials were very low (−2.6 to −6.0 MPa), but rose by circa 2 MPa within a day after the irrigation. Thus, water was effectively acquired by the shallow roots in the wetted zone. Both the root tissue and adjacent sand samples collected below the wetting front exhibited a pronounced deuterium enrichment in almost all cases. The deuterium enrichment decreased with soil depth apparently due to dilution with existing tissue water. A dilution was also observed from the roots to the soil, although the water content of soils was very low (< 0.8% by mass). This result indicates that there was water flux below the wetting front through the roots and into the sand surrounding the roots (Fig. 1). Diffusion of the deuterium-labelled water directly through the very dry sand would be orders of magnitude too slow to appear at these depths 50–100 cm below the wetting front in this period of time (Richards and Caldwell 1987). There was no significant macropore flow apparent when the pits were excavated to collect the sand and root samples.

Discussion

This is the first demonstration of inverse hydraulic lift using an isotopic tracer under field conditions. This process may be the mechanism responsible for the occurrence of very deep roots in many water-limited ecosystems of the earth. The importance of deep roots for species of water-limited environments is obvious, but beyond the benefits for individual plants, ecosystem-level implications are being appreciated. Since root system biomass is largely in upper soil layers and then

Fig. 1 Deuterium enrichment in roots and adjacent sand. Two plants of each of three species, *Stipagrostis amabilis*, *Stipagrostis obtusa*, and *Centropodium glauca* were surface irrigated with 3–5 l water (corresponding to 25–30 mm precipitation) which included 100 ml 99.9% D_2O. Water from the sample was subsequently vacuum extracted and isotope ratios measured by mass spectrometry. Deuterium enrichment is expressed as $\log_{10}$ δD minus the background δD (Standard Mean Ocean Water) of sand in an adjacent profile. Root and soil samples occurring at the same depth were collected adjacent to one another



normally tapers sharply with depth, deep roots were included in hydrological and biogeochemical models only recently (Knorr and Heimann 1995; Jackson et al. 1996). Even at the global level, models that take deep roots into account yield more realistic predictions of biome evapotranspiration, river discharges and feedbacks to the atmosphere (Kleidon and Heimann 1996, 1998). Roots that penetrate to considerable depth also have important implications for ecosystem carbon storage (Nepstar et al. 1994). Nevertheless, roots require a mechanism for penetrating dry soil layers in their downward growth in water-limited ecosystems. Inverse hydraulic lift, as demonstrated here, may be that mechanism.

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