

## REPORT

# Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift

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## Abstract

Under large East African *Acacia* trees, which were known to show hydraulic lift, we experimentally tested whether tree roots facilitate grass production or compete with grasses for below-ground resources. Prevention of tree–grass interactions through root trenching led to increased soil water content indicating that trees took up more water from the topsoil than they exuded via hydraulic lift. Biomass was higher in trenched plots compared to controls probably because of reduced competition for water. Stable isotope analyses of plant and source water showed that grasses which competed with trees used a greater proportion of deep water compared with grasses in trenched plots. Grasses therefore used hydraulically lifted water provided by trees, or took up deep soil water directly by growing deeper roots when competition with trees occurred. We conclude that any facilitative effect of hydraulic lift for neighbouring species may easily be overwhelmed by water competition in (semi-) arid regions.

## Keywords

*Acacia tortilis*, facilitation, soil water, stable isotopes, tree–grass interactions.

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## INTRODUCTION

Savanna ecosystems are characterized by a continuous grass layer interspersed with trees and shrubs. A number of studies has focused on the interactions between the grasses and woody species in savannas but definitive experiments demonstrating how plant–plant interactions are influenced by water competition and/or facilitation have been few. Traditionally, the co-occurrence of trees and grasses in savannas is explained by niche partitioning. Walter (1971) proposed that trees have sole access to water in deeper soil layers while grasses are the dominant competitor for water in the upper soil layers. This model of co-existence is called the two-layer hypothesis. Evidence exists supporting the two-layer hypothesis (Hesla *et al.* 1985; Knoop & Walker 1985; Sala *et al.* 1989), although several recent studies have rejected it (Le Roux *et al.* 1995; Seghier 1995; Mordelet *et al.* 1997) in light of a growing body of evidence showing that trees may facilitate understorey grass production (Joffre & Rambal 1988; Weltzin & Coughenour 1990; Bertness &

Callaway 1994; Bruno *et al.* 2003). Particularly in East African savannas, grass productivity may be higher under trees (Belsky *et al.* 1989; McClaren & Bartolome 1989; Weltzin & Coughenour 1990) which is commonly attributed to increased soil nutrient concentrations (Belsky 1994).

Another mechanism by which trees can facilitate understorey productivity is through hydraulic lift. Hydraulic lift is the process of water movement upwards from relatively wet to dry soil layers through the roots of plants that have access to both deep and shallow soil layers (Richards & Caldwell 1987; Caldwell *et al.* 1998). Except for CAM plants (Yoder & Nowak 1999), this transport takes place during the night when leaf stomata are closed and the major water potential gradient is between deep (wet) roots and drier surface roots present in the top soil (Richards & Caldwell 1987). Several authors have suggested that hydraulic lift may have substantial community and/or ecosystem effects (Caldwell *et al.* 1998; Jackson *et al.* 2000; Horton & Hart 1998; Meinzer *et al.* 2001). Hydraulic lift could increase productivity of neighbouring species and a higher soil moisture

content of the topsoil could increase nutrient cycling (Dawson 1993, Caldwell *et al.* 1998). However, there have been very few empirical studies that have demonstrated the effects of hydraulic lift on community and/or ecosystem structure or function. If facilitation via hydraulic lift of understorey plants by savanna trees does exist, this process could have a large impact on the productivity of savannas. Ecosystem productivity in turn is very important for the rest of the food web in African savannas which supports tremendous amounts of animal biomass and diversity (Olf *et al.* 2002).

Previously, we have shown that hydraulic lift occurs in *Acacia tortilis* (Forsk.) trees in an East African savanna. Mature *Acacia* trees may lift and exude between 75 and 225 L of water each night to an area of more than 300 m<sup>2</sup> (Ludwig *et al.* 2003). Analyses of oxygen isotopes of xylem water indicated that grasses growing near trees take up hydraulically lifted water. However, at this same site moisture content of the topsoil was lower under trees compared with the open grassland (Ludwig *et al.* 2004). This suggests that water use by the trees and grasses together is very high and therefore the potential for competition between them is also high (Ludwig 2001). These observations stimulated us to ask the question what the consequences are of hydraulic lift for understorey grass productivity.

Three hypothesis are possible explaining below-ground interaction between trees and grasses: (i) trees could facilitate grass production through hydraulic lift; (ii) trees and grasses can compete for below-ground resources or (iii) there is niche separation of rooting depth as explained by the two layer hypothesis.

These hypotheses were tested with a field experiment in Tanzania, East Africa, in which we directly prevented tree–grass root interactions via root trenching. We expect that (i) if below-ground competition overwhelms facilitative effects of hydraulic lift root trenching will increase understorey grass production, (ii) alternatively, if facilitation through hydraulic lift dominates below-ground interactions root trenching will reduce grass production, or (iii) if there is niche separation of trees and grasses, root trenching will have an insignificant effect on grass production. The latter is expected because, according to the two-layer hypothesis, grasses are the superior competitors for water in the topsoil while trees extract most of their water from deeper soil layers. To test these predictions we measured aboveground biomass, soil water content in control plots and plots around which all tree roots were trenched. Plant nutrient concentrations were determined to check whether differential nutrient availability occurred as a result of trenching. In addition, we measured the oxygen stable isotope composition of water in trees, grasses, soils, rain and ground water to determine whether root trenching changed water source for grasses.

## MATERIALS AND METHODS

### Site description and experimental design

The experimental trees were located in the northern part of Tarangire National Park (4° S, 37° E, 1200 m a.s.l.) in northern Tanzania. The soil at the site consisted of coarse sandy loams of lacustrine origin. The vegetation is wooded savanna with a tree cover of 10–20%. The dominant tree species is *Acacia tortilis*, the tree we used in our experiments. The herbaceous layer under tree canopies is dominated by C<sub>4</sub>-perennial grasses. The dominant grass species is *Cynodon dactylon* (L.) (62% cover) and two other common species are *Panicum maximum* (Jacq.) (9%) and *Cenchrus ciliaris* (L.) (9%). Mean rainfall is 650 mm year<sup>-1</sup> (SD = 272 mm) and the wet season occurs from November until May. During the first year of our study (1999), rainfall was above average (750 mm) and stopped half way in May. In 1999, especially April was very wet with 350 mm rain in 1 month. The second year (2000) of the study was very dry with only 350 mm of rain that stopped early (by late April).

The study area is located in the dry season range of large migratory herbivore populations. From June until December, the site is grazed by large herds of Burchell's zebra (*Equus burchelli* Gray) and wildebeest (*Connochaetes taurinus*). In the wet season, most of the herbivores migrate to the Masai Steppe (Voeten & Prins 1999) and as a result from January until June (wet season), there is only occasional grazing by impala (*Aepyceros melampus*) and herds of African elephant (*Loxodonta africana*) moving through the area.

Previous work showed that during the dry season of 1998, all trees showed hydraulic lift and trees exuded between 75 and 225 L of water each night (Ludwig *et al.* 2003). The wet season of 1998 was very wet with double the average rainfall. During the dry season of 2000, a very dry year, there were very few indications of hydraulic lift from mid-May until 3 months later in the dry season (Ludwig *et al.* 2003). From 1999, fewer data is available because of equipment failure. However, the three series of data collected during the first 3 weeks of June 1999 show similar hydraulic lift patterns as in 1998, probably because 1999 was also a relatively wet year (Ludwig 2001; F. Ludwig, unpublished data).

For the experiments, we used four large isolated *A. tortilis* trees which were all approximately 100 years old (Prins & Van der Jeugd 1993). The trees had an average dbh of 59 (SD = 19) cm and a canopy diameter of 15–20 m. To test the effects of hydraulic lift on grass production under each tree four plots of 3 by 3 m were laid out in four compass directions. Two plots per tree were randomly assigned as control. Around the other two plots at the two sides closest to the target tree, we dug trenches until we reached a hard pan layer at a depth of

60–80 cm. Although tropical grasses are known to root below 60–80 cm, this is unlikely for *Cynodon dactylon*, the species that dominated the vegetation under these *Acacia* trees. This lawn-forming grass species usually does not grow roots below 80 cm (Anderson & Herlocker 1973; Carrow 1996; Franzluebbers *et al.* 2002). A study of the rooting depth of *C. dactylon* in Lake Manyara NP, a park close to the study area with similar vegetation and rainfall pattern never demonstrated any roots of this species below 50 cm (Prins 1996; H.H.T. Prins, unpublished data). This rooting pattern in combination with the presence of the hard pan makes it unlikely that the grasses rooted in the soil layers below the hard pan and assures that nearly all grass–tree root interactions were prevented in the trenching treatment. Soil was removed from the trenches for the first time in April 1999; after which the trenches were refilled with the same soil that had been removed. At the time of trenching, soil water content was at field capacity because of the high rainfall in April. The trenching treatment was repeated in April 2000. There was little new root growth after the first year (1999) and within all eight plots only one large tree root had re-grown into one of the adjacent grass plots. To avoid possible edge effects, we only used the inner 2 by 2 m of the plots; one half of each plot was used to determine plant biomass and the other half was used to determine soil and plant water contents.

#### Soil water contents, aboveground biomass and plant nutrient concentrations

To test how hydraulic lift influence plant available water, we determined soil moisture content in trenched and control plots. Therefore, in each plot we took two soil samples which were divided in two different depths from 0 to 10 cm and 20–30 cm. Soil water content in samples was determined gravimetrically by drying them at 100 °C. In 1999, soil samples were collected on four different dates starting on June 3 and ending on August 13 and on three dates in 2000 between May 12 and July 17.

Around each 2 × 1 m subplot used for the above-ground biomass measurements, we constructed a chain-link enclosure to prevent grazing by large herbivores. These subplots were further divided into three sampling plots of 100 × 67 cm. On each sampling date, one of these sampling plots was hand-clipped to ground level and plant material was sorted into live (green) and dead (non-green) grasses and herbs. Plants were dried in the sun for several days and then weighed. During the first harvest in 1999, plant material was only sorted by plant type (herbs and grasses). In both years, aboveground biomass was determined 2, 8 and 14 weeks after the last rainfall event.

N/P ratios of plant tissues in this system have been shown to be good indicators of which nutrient limits the production of the vegetation (Koerselman & Meuleman 1996; Ludwig *et al.* 2001). A nutrient addition experiment indicated that under trees, grass production is limited by P and not by N and that P fertilization reduced grass N : P ratios (Ludwig *et al.* 2001). If trees and grasses compete severely for the limiting nutrient (i.e. phosphorus), we expect that the elimination of below-ground competition root trenching will also reduce N : P ratios because of higher P concentration in the grass tissue. In order to test whether root trenching affected potential nutrient limitations, a subsample of the grass biomass taken in 2000 was analysed for total N and P concentration. N and P tissue concentrations were determined using a modified Kjeldahl procedure with selenium as a catalyst (Novozamski *et al.* 1983).

#### Stable isotope sampling

Variation in the oxygen and hydrogen stable isotope composition of source waters can be used to determine the zone of active water uptake by plant roots (Ehleringer & Dawson 1992; Dawson *et al.* 2002). Therefore, in 2000, we collected grass, tree, soil, rain and ground water samples for oxygen stable isotope composition. Groundwater was obtained from two different bore (well) holes, one about 500 m and another at 5 km from the experimental trees. In addition, during the wet season of 2000 between January and April, we collected 14 different rain samples. Isotope composition of rain and ground water come from a previously published paper by Ludwig *et al.* (2003).

In each plot, we collected one soil sample at a depth of 25–35 cm and at least one sample from the dominant grass species, *Cynodon dactylon*. From every tree we took root and stem samples to determine water sources of the trees following the methods outlined by Dawson & Ehleringer (1993). All plant and soil samples for isotope analysis were collected between 7 and 9 June 2000 which was 4 weeks into the dry season.

Water was extracted from soil and plant tissue using a cryogenic vacuum distillation apparatus (Ehleringer *et al.* 2000). 500 µL of the extracted water was injected into airtight vials flushed with 2000 or 3000 ppm CO<sub>2</sub> in He. After 48 h, CO<sub>2</sub> in the head space was analysed for its oxygen isotope ratio with a Finnigan MAT Delta<sup>plus</sup> XL isotope mass spectrometer (IRMS) interfaced with a GasBench II and PAL-80 autosampler following the method outlined by Tu *et al.* (2001). All δ<sup>18</sup>O values are expressed in delta notation (‰) relative to an accepted international standard (V-SMOW) (see Ehleringer & Dawson 1992). Overall precisions for all isotope runs was ±0.18‰.

## Statistical analysis

Soil water content, plant nutrient concentration, total aboveground biomass, herb biomass and life, dead and total grass biomass were analysed with a repeated measures ANOVA with trenching treatment as a fixed factor, trees as a random factor, and date as the repeated factor. In case of the soil water content, soil depth was taken as an additional fixed factor. The effects of compass direction of plots on plant biomass and soil water content was not significant, so this factor was eliminated from the final statistical analyses.  $\delta^{18}\text{O}$  values in soil and grass water was analysed with an ANOVA using trenching treatment as a fixed factor and trees as a random factor. All data were statistically analysed with SPSS 10.0 for Windows.

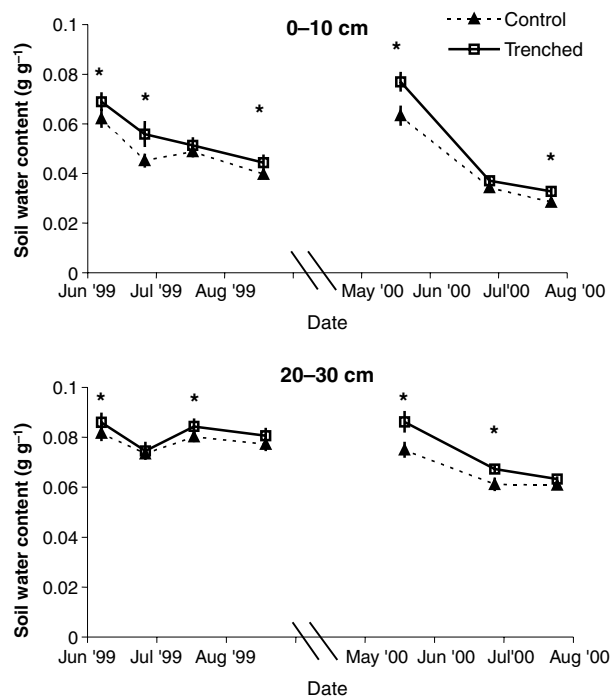
## RESULTS

### Soil water content, aboveground biomass and plant nutrient concentration

During both years of the experiment, removing the effects of tree roots in the trenched plots resulted in a higher soil water content compared with control plots (Fig. 1; Table 1). This was the case for both soil depths but effects of trenching on soil water content were greater near the soil surface.

In trenched plots, total aboveground biomass was significantly higher than in control plots (Fig. 2, Table 1). In 1999, biomass was higher in trenched plots during the entire measurement period. In 2000, however, biomass was only higher at the end of the wet season; at 8 and 14 weeks into the dry season these differences were no longer significant. The year 2000 was an extremely dry year and therefore plant growth was depressed and was relatively low compared with 1999 (Fig. 2). Grass biomass followed the same trend as total biomass with a higher production in the trenched plots. In 1999, about 10–20% of aboveground biomass measured was from herbs but herbs did not respond as strongly to the trenching, as did the grasses. In 2000, herb biomass was negligible. The amount of live grass was also significantly higher in the trenched plots while dead grass biomass was not significantly affected by trenching (Fig. 2, Table 1).

Plant nutrient concentrations and N : P ratios were never significantly different between trenched and control plots (Table 2). Grass nitrogen concentration decreased over time but N : P ratio remained stable throughout the season and was about 13 both in trenched and control plots.



**Figure 1** Effects of root trenching on soil water content under *Acacia tortilis* trees. Soil water content was determined in plots, which were surrounded by root trenches and compared with control plots. Soil samples were taken from two different soil layers (0–10 and 20–30 cm) during the first 3 months of the dry season for 2 years. Data are averages  $\pm$  SE and asterisks indicate a significant effect of root trenching on soil water content on that individual date.

### Stable isotopes

$\delta^{18}\text{O}$  values of precipitation were on average  $-2\text{‰}$  (Fig. 3). There was some variation in the isotopic values of rainfall which was mainly because of the type of rainfall event; as expected water collected during relatively heavy rainfall events had more depleted (lower) values while lighter rainfall events showed more enriched (higher) values (see Dawson 1993). The  $\delta^{18}\text{O}$  of water collected from both bore holes (ground water) at the site showed nearly identical isotopic values ( $-3.9\text{‰}$ ). Soil water  $\delta^{18}\text{O}$  values were highly enriched which was probably because of evaporation. Mean  $\delta^{18}\text{O}$  value in soil from control plots was  $+0.5\text{‰}$  and slightly higher than in trenched plots ( $-0.1\text{‰}$ ) but these differences were not significant. The isotopic value of water extracted from tree roots and stems was similar to that obtained from the ground water which indicates that, 1 month into the dry season, trees used ground water and not water from the topsoil. Water extracted from the grasses growing in control plots showed the same isotopic value as tree roots while grasses from trenched plots had significantly higher values

**Table 1** Results of a general linear model testing the effects of root trenching on soil water contents, above ground biomass (all by repeated measures ANOVA) and  $\delta^{18}\text{O}$  values in grass and soil water (by ANOVA). Presented are  $F$ -values and levels of significance. Aboveground biomass and soil water contents were determined during both years of the experiment;  $\delta^{18}\text{O}$  values in plant and soil water only during the second year of the experiment

	Soil water content		Aboveground biomass						$\delta^{18}\text{O}$		
	d.f.	$F$	d.f.	Total ( $F$ )	Total grass ( $F$ )	Dead grass ( $F$ )	Herbs ( $F$ )	Live grass ( $F$ )	d.f.	Grasses ( $F$ )	Soil ( $F$ )
Date (Da)	6	5.7*	5	24.6**	21.9***	10.3*	6.5*	10.8***			
Trenching (Tr)	1	20.4**	1	5.8*	6.2*	0.5	0.3	4.3*	1	5.9*	1.1
Tree	3	113.1***	3	4.3**	11.1***	7.2***	2.9*	6.5*	3	0.4	1.0
Depth (De)	1	55.7***									
Tr $\times$ Da	5	2.9	5	0.7	0.6	1.2	1.2	1.1			
De $\times$ Da	6	22.4***									
Tr $\times$ De	1	1.7									
Tr $\times$ De $\times$ Da	6	0.8									

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

more like rainfall. Hence, grasses switched to a different water source as a result of tree root trenching.

## DISCUSSION

In a previous study, we showed that large, mature, *A. tortilis* trees in East African savannas conduct hydraulic lift and that significant amounts of water are redistributed to the topsoil each night (Ludwig *et al.* 2003). In the present paper, we report our results on the effects of hydraulic lift on tree–grass interactions with a root trenching experiment to test whether hydraulic lift can facilitate the productivity of understorey grasses. Severing tree roots to remove the positive effects of hydraulic lift on soil moisture content had the opposite effect from what we expected; soil water content was higher in the trenched plots relative to the controls. This demonstrated that trees took up more water from the topsoil than they lost and that below-ground competition overwhelmed the facilitative effects of hydraulic lift.

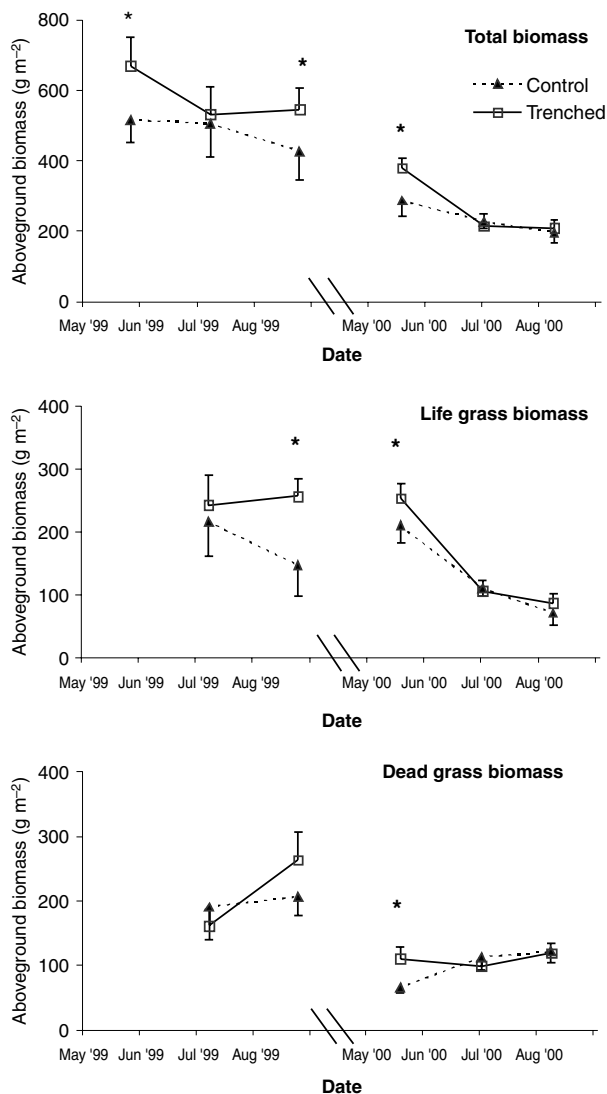
During both years of our experiment, grass biomass was higher in trenched plots compared with control plots indicating that grasses benefited from reduced competition with trees. In addition, the fact that there was more live biomass and a higher live/dead ratio in trenched plots suggests that grasses had more water available and therefore grew more in trenched plots. This shows that below-ground interactions between trees and grasses are dominated by competition and not facilitation.

Several authors have suggested that hydraulic lift can have substantial ecosystem effects and that water lifting trees would facilitate understorey plants in a number of ways

(Caldwell *et al.* 1998; Horton *et al.* 2001). Our study shows that in a system where hydraulic lift occurs, water competition may overwhelm the positive effects of hydraulic lift. Actually, we are aware of only one case (*Acer saccharum* trees in the eastern United States) where hydraulic lift caused a higher soil water content under trees compared with soil outside trees (Dawson 1993). Here, understorey grasses had a higher plant water potential and stomatal conductance if they took up more hydraulically lifted water (Dawson 1993). Facilitative effects may thus overwhelm competition for water. However, the positive effects of hydraulic lift were observed in an ecosystem which is much less limited by water than the East African semi-arid savanna that we studied.

Our results show that trees extracted significant amounts of water from the topsoil. In addition, most of the rooting distribution data of savannas shows that trees have most of their roots in the topsoil probably because in the topsoil nutrients and water co-occur (Scholes & Archer 1997). When trees and grasses have most of their roots in the topsoil, it is very likely that trees and grasses will interact and in some cases compete for water in the topsoil. This type of interaction indicates that there is no complete niche separation of rooting zones between trees and grasses; our results add to an increasing number of studies suggesting that the two-layer hypothesis cannot always explain competitive interactions in savannas (Le Roux *et al.* 1995; Mordelet *et al.* 1997; Higgins *et al.* 2000).

While below-ground competition in our study was most likely for water, we cannot eliminate the possibility that trenching may have also reduced competition for soil



**Figure 2** The effects of root trenching on total, and live and dead grass aboveground biomass under *Acacia tortilis* trees. Biomass was measured in plots which were surrounded by root trenches and compared with control plots during the first 3 months of the dry season for 2 years. Data are averages  $\pm$  SE and asterisks indicate a significant effect of root trenching on plant biomass on that individual date.

nutrients. However, foliar nutrient concentrations and the N : P ratios in aboveground biomass of the herbaceous layer were not affected by root trenching. A previous study showed that P is the limiting nutrient for grasses growing under trees and that P fertilization changed the N : P ratios of the grasses (Ludwig *et al.* 2001). So, if biomass in trenched plots was higher because of reduced competition for P, then N : P ratios would have changed as well. As this did not occur, competition for soil nutrients between trees and grasses was probably minimal. Alternatively, as grasses

are likely to be the superior competitor for P compared with woody species in dry environments (Black *et al.* 1994; Yoder & Nowak 2000), even if competition below-ground was alleviated, it probably did not affect grass production. In all, our results thus suggest that grass growth was reduced through the indirect effects of below-ground competition for water.

Although effects of water competition between trees and grasses probably prevailed in this study, it is still possible that the understorey vegetation received some benefits from hydraulic lift. The isotope data obtained, in July 2000, from grasses growing in control and trenched plots show that root trenching changed the water source of the grasses. In trenched plots, grasses used a water source with an isotopic signature similar to rainfall but in control plots grasses used a water source similar to groundwater, which could be water hydraulically lifted by trees. However, soil isotope data showed no change in isotope composition because of trenching. One explanation for this discrepancy may be that water is transferred from tree roots to grasses through root grafting or close associations between roots of trees and grasses. This would have allowed water transfer without a shift in the isotopic composition of soil water but to our knowledge such tree–grass root associations have never been described. Querejeta *et al.* (2003), however, showed possible nocturnal water transport through roots to mycorrhiza. If the grasses and trees share the same mycorrhiza, these could have facilitated water transport between the two. It is also possible that grass roots are closely associated with tree roots. If grass roots grow along the roots of trees, they could take up hydraulically lifted water before it moves further into the soil.

An alternative explanation for the grass isotope data is that under control conditions, grasses used a deeper soil water source themselves, with an isotopic signature similar to groundwater, and switched to a more shallow water source when tree root activity is eliminated. However, given the fact that there was a hardpan at 60–80 cm through which the dominant shallow-rooting grass species, *Cynodon dactylon*, that rarely ever roots below 40 cm (Hitchcock & Chase 1971) would have to penetrate, it seems very unlikely that grasses can access deeper water sources themselves.

The occurrence of hydraulic lift in this savanna ecosystem suggested that trees facilitate the understorey vegetation by increasing water availability; however, the results of this trenching experiment show that trees also compete with grasses for below-ground resources. It thus appears that trees facilitate and compete with grasses simultaneously. Lately, several studies have shown that plant interactions commonly include both positive and negative effects (Callaway & Walker 1997; Holzapfel & Mahall 1999; Callaway & Pennings 2000; Ludwig *et al.* 2004). This tropical semi-arid savanna is another example of an

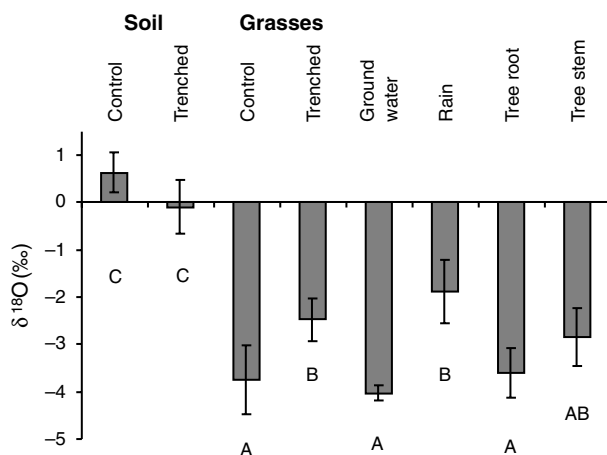
**Table 2** The effect of root trenching on plant total N and P concentration and N : P ratio. Nutrient concentrations were determined from plants collected in plots which were surrounded by root trenches and compared with control plots during the first 3 months of the dry season. Data are averages  $\pm$  SE ( $n = 8$ ). (b) Results of repeated measures ANOVA on the effect of root trenching on N and P concentration and N : P ratio in grass tissue

(a) Concentrations						
	N		P		N : P ratio	
	Trenched	Control	Trenched	Control	Trenched	Control
16 May 2002	18.8 (1.0)	18.7 (1.3)	1.42 (0.07)	1.64 (0.11)	13.4 (0.7)	11.9 (1.3)
28 June 2002	15.2 (1.4)	15.0 (1.4)	1.27 (0.06)	1.32 (0.13)	12.1 (1.2)	11.9 (1.1)
4 August 2002	14.9 (1.6)	15.5 (1.6)	1.15 (0.10)	1.10 (0.12)	13.9 (1.7)	13.9 (1.7)

(b) <i>F</i> values				
	d.f.	N	P	N : P ratio
Date	2	79.2*	8.8	4.6
Trenching	1	0.2	0.9	0.5
Tree (block)	3	1.2	6.7**	3.6*
Date $\times$ trenching	3	0.1	1.3	0.4

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .



**Figure 3** Mean  $\delta^{18}\text{O}$  values (‰, with bars indicating  $\pm$  SE) of rain and ground water and in tree twigs and roots of *Acacia tortilis* trees. These values were compared with water in soil and grasses in plots, which were surrounded by root trenches and in control plots. Samples were collected 1 month into the dry season between 7 and 9 July 2000. Bars with the same letter are not significantly different (LSD test,  $P > 0.05$ ).

ecosystem where both competition and facilitation can occur at the same time. Not only do trees have both positive and negative effects on grass water availability, they also facilitate grass growth through increased nutrient availability and trees reduce grass production during the wet season as a result of shade (Ludwig *et al.* 2001, 2004) Whether the net effect of these complex interactions is positive or negative depends on a range of factors and could change from year

to year. For example, during 1998 (a very wet year), trees showed much more hydraulic lift than during 2000, a dry year, indicating that facilitation might be more important during relatively wet years (Ludwig *et al.* 2003). However, based on the data of two different years of our study, we conclude that beneficial effects of hydraulic lift for understorey species in semi-arid areas are probably limited and that below-ground competition for water is usually the most important process in savanna ecosystems.

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