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Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California Oak savanna

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Abstract

Many studies have shown that the total abundance of hyphae in the soil covaries seasonally with soil moisture. We investigated the extent to which soil hyphal abundance varies as a function of depth and moisture availability within the soil profile during the dry season, and determined whether soil moisture compensation via hydraulic lift (HL) buffers rhizosphere fungi from the effects of severe soil drying. We measured soil water potential, isotopic composition of soil water and total hyphal length in a California coast live oak stand and adjacent grassland at the beginning and end of the 5-month summer drought period. Throughout the summer, oaks maintained predawn water potential values (-0.4 ± 0.1 MPa) that were significantly above those recorded in the 0–200 cm soil depth interval, strongly suggesting root access to groundwater. Direct evaporation of soil water was much more intense and affected deeper layers of the profile in the grassland compared to the oak stand, as indicated by extremely negative water potential values and very enriched isotopic composition of soil water near the surface. Significantly higher soil water potential and less isotopically enriched soil water at 15–40 cm depth in the oak stand were consistent with oak root exudation of isotopically depleted groundwater or deep soil water not exposed to evaporation. Hyphal length in the soil profile declined markedly during the summer drought period in the grassland, particularly in upper layers (41–75% decrease at 0–40 cm depth), indicating rapid turnover of the arbuscular mycorrhizae (AMF) dominated hyphal carbon pool after grass senescence. By contrast, soil hyphal length in the ectomycorrhizal (EM)/AM oak stand remained remarkably constant throughout the summer drought period, with the only exception of the topsoil layer exposed to direct evaporation (49% decrease at 5 cm depth). The sustained exudation of water from roots to soil through HL may have buffered rhizosphere hyphae against the negative effects of extreme soil desiccation in the oak stand. These data suggest that HL by deep-rooted trees may influence the biogeochemical cycling of carbon and nutrients in seasonally dry ecosystems through effects on rhizosphere fungi.

Keywords: *Quercus agrifolia*; *Bromus* sp.; Soil moisture; Drought; Hydraulic lift; Stable isotopes; Soil hyphal length; Ectomycorrhizae; Arbuscular mycorrhizae

1. Introduction

The total length of fungal mycelium in the soil has been found to fluctuate seasonally in a wide range of natural ecosystems (Hunt and Fogel, 1983; Osono et al., 2003; Staddon et al., 2003b; Li et al., 2005). Much of this variation is attributable to the influence of abiotic factors such as soil moisture and temperature. Many studies have indicated that soil hyphal length and biomass covary with soil moisture (Berg et al., 1998; Morris and Boerner, 1999; Frey et al., 1999; Osono et al., 2003; Allen et al., 2005) and that declines in mycelial abundance during drought periods may be linked to both plant and soil factors (Hunt and Fogel, 1983; Staddon et al., 2003b). The negative impact of

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drought on fungal mycelia has two components—the direct effects of soil desiccation on hyphae (Juniper and Abbott, 1993), and indirectly, via changes in net primary productivity and carbon allocation from the host plant to mycorrhizal fungi (Egerton-Warburton, unpublished data).

Research on the spatial (within site) and temporal (seasonal) fluctuations in hyphal standing biomass in the soil is needed to improve our understanding of carbon and nutrient cycling in seasonally dry ecosystems (Fogel and Hunt, 1979, 1983). The present study was conducted in a coast live oak (*Quercus agrifolia* Nee) savanna in a warm Mediterranean-type ecosystem characterised by a prolonged summer drought period, and where seasonal fluctuations in soil hyphal abundance might be expected to be large. We investigated how the total standing biomass of hyphae in the upper two meters of the soil profile responds to horizontal and vertical gradients in soil moisture that develop during the dry season in this ecosystem. Few studies have looked at hyphal abundance in the entire soil profile, as most of them concentrate in the upper 10–30 cm of soil only. However hyphae in deeper layers of the profile may represent a significant proportion of total fungal biomass in plant rhizospheres (Hunt and Fogel, 1983), and mycorrhizal hyphae colonizing deep soil or bedrock may be functionally important for host plants (Egerton-Warburton et al., 2003; Bornyasz et al., 2005).

Hyphal persistence in the soil is determined by its active lifespan and, once dead, the decomposition rate. Analyses of carbon-14 content have shown that most extramatrical hyphae of AM fungi live, on average, 5–6 days (Staddon et al., 2003a), although their lifespan may be longer (14–21 days) under certain conditions (Egerton-Warburton, unpublished data). Turnover of some of the extraradical hyphae of AM fungi appears to be on the order of weeks (Friese and Allen, 1991; Staddon et al., 2003a, b; Steinberg and Rillig, 2003), although other components of the mycelium such as runner hyphae (Friese and Allen, 1991) may turn over more slowly. Several authors have suggested that the lifespan of EM hyphae could be longer, and the decomposition rate could be slower, than that of AM hyphae (Langley and Hungate, 2003; Treseder et al., 2005). However, Hunt and Fogel (1983) found that the total length of soil hyphae in an EM dominated coniferous forest decreased over threefold within 4 months during the summer dry period, which indicates a rather fast turnover rate of EM mycelia. Likewise, Bååth et al. (2004) estimated that 60–70% of EM hyphae in the soil of a Swedish mixed forest decomposed within 3–6 months after carbon supply from host plant was interrupted. The decomposition rate of dead fungal mycelia would be expected to be fast at the extremely high average and peak temperatures reached during the summer in Southern California, which would lead to sharp declines in the total standing biomass of hyphae in the soil unless most hyphae remain alive and/or new hyphae are produced to replace the decaying mycelia. Further, dead or senescent mycorrhizal mycelia are preferentially grazed by mycophagous microarthropods (e.g., collembola; Kaneda and Kaneko, 2004), so total soil hyphal length would be expected to decline abruptly during the summer drought period in this California savanna ecosystem unless extraradical mycorrhizal hyphae remain alive and/or new hyphae are produced.

Very little is known about the potential relationship between hyphal abundance and hydraulic lift (or redistribution), the passive transfer of water from deeper soils into the dry upper soil layers by roots during the night (Dawson, 1993; Caldwell et al., 1998). The exudation of hydraulically lifted water into dry upper soil layers might protect fungal hyphae against extreme soil desiccation, as suggested by Caldwell et al. (1998). Moreover, the direct transfer of water from the host plant to the extraradical mycorrhizal mycelium might also contribute to maintaining the integrity and functionality of mycorrhizal hyphae in dry soils (Querejeta et al., 2003). Coast live oaks and other native California oak species have been shown to conduct hydraulic lift during dry periods (Ishikawa and Bledsoe, 2000; Querejeta et al., 2003). Further, *Q. agrifolia* forms mutualisms with the two major mycorrhizal groups, arbuscular (AMF) and ecto-mycorrhizal fungi (EM; Egerton-Warburton and Allen, 2001), which makes it a good model species to study the effects of hydraulic redistribution on rhizosphere hyphal abundance during drought.

This study has two objectives: to assess how soil hyphal abundance varies as a function of depth and moisture availability within the soil profile during the dry season, and to determine whether soil moisture compensation via hydraulic lift buffers rhizosphere fungi from the effects of extreme soil drying. The study was conducted during an exceptionally dry spell in Southern California (years 1999–2002 with annual precipitation well below average). We measured total hyphal length and soil water potentials in a California coast live oak stand and adjacent AMF-dominated grassland at the beginning and end of the 5-month summer drought period. We also measured the isotopic composition of soil water in subsurface soil layers (10–40 cm) in the late dry season to look for evidence of root exudation of deep water not exposed to evaporative isotopic enrichment (Dawson, 1993; Caldwell et al., 1998).

2. Materials and methods

The study was carried out in Lopez Canyon in the Western Riverside County Multispecies Reserve (33°39′18″N, 116°59′49″W) in Southern California. The area has a Mediterranean-type climate with 270 mm precipitation annually (30 year mean), most falling between November to April. This study occurred during the dry period of a below-average precipitation year. During the two growing seasons prior to this study the precipitation was below average (Table 1). Because soil temperatures and maximum temperatures are high and relative humidity low, evapotranspiration demand exceeds precipitation. Soils are largely decomposed granites in the valley bottoms

Table 1
Monthly average temperatures (air maximum and minimum and soil temperature) and evapotranspirational demand and precipitation leading up to and during the study

Month-Year	Total evapot (mm)	Total precip (mm)	Average T^{max} (°C)	Average T^{min} (°C)	Average T^{soil} (°C)
Jul-99	196	0	31	13	27
Aug-99	199	0	32	13	24
Sep-99	135	0	30	11	21
Oct-99	133	0	31	9	18
Nov-99	74	0	24	5	14
Dec-99	71	0	21	2	9
Jan-00	62	0	20	4	9
Feb-00	63	18	18	6	10
Mar-00	102	21	20	5	11
Apr-00	144	19	24	7	13
May-00	173	0	27	9	16
Jun-00	206	0	30	11	19
Jul-00	229	0	32	12	20
Aug-00	202	1	32	15	20
Sep-00	158	8	30	13	18
Oct-00	94	17	23	10	14
Nov-00	74	4	20	3	8
Dec-00	67	0	22	3	7
Jan-01	56	24	16	2	5
Feb-01	60	80	16	3	6
Mar-01	104	19	20	6	15
Apr-01	133	25	20	6	16
May-01	186	2	27	11	23
Jun-01	208	0	30	12	24
Jul-01	197	0	31	12	23
Aug-01	195	0	33	14	24
Sep-01	156	0	32	12	22
Oct-01	113	1	28	10	18

Source data: California Irrigation Management Information System, Temecula East station, www.cimis.water.ca.gov.

with rocky granitic outcroppings. The valley bottoms are dominated by exotic annual grasses introduced from the Mediterranean, especially species of *Bromus* with interspersed individuals and stands of coast live oak (*Q. agrifolia* Nee) and Engelmann oak (*Q. engelmannii* Greene). Agriculture and grazing in the area ended in the mid-1980s and the land was annexed to the Reserve to increase habitat for rare and endangered species.

On 31 May 2001 and 17 October 2001, soil profiles were collected using a 9 cm-diameter bucket auger from the soil surface to a depth of 200 cm at 10–15 cm increments. Three soil profiles were sampled at an oak stand, and another three profiles were taken in an adjacent grassland site (within 25 m of the stand). Water for stable isotope analyses was extracted from soil samples using a cryogenic vacuum distillation line (Ehleringer and Osmond, 1989). Stable isotope analyses of soil water were conducted at the Stable Isotope Laboratory of the Department of Earth and Planetary Sciences, University of New Mexico. Hydrogen isotope ratios were determined using a continuous flow high temperature reduction technique (Sharp et al., 2001). One-microliter aliquots of water are injected into a helium stream through a heated septum. The vaporized sample is reduced to CO and H_2 while passing through a graphite column heated to 1450 °C. Reactant gases are purified by passage through a gas chromatography column, through a Finnigan MAT CONFLO II interface/open split for helium dilution, and into a Finnigan MAT Delta XL Plus mass spectrometer. Data are reported in conventional delta notation, defined as the per mille (‰) deviation from SMOW (Vienna standard mean ocean water):

$$\delta D = [(R_{\text{sample}} - R_{\text{SMOW}})/R_{\text{SMOW}}] \times 1000,$$

where R_{sample} and R_{standard} are the D/H ratios in the samples and the standard, respectively. δD measurements had a precision of ± 2‰.

Oxygen isotope ratios in waters were determined using the CO_2 equilibration technique. The water samples (1 ml each) were injected in borosilicate vials equipped with rubber septa, which were previously purged with He–CO_2 gas mixture (0.5% CO_2). After 24 h equilibration at 25 °C, the CO_2 was measured by continuous flow isotope ratio mass spectrometry using an automated CombiPal—Gas Bench system coupled to a Finnigan Mat Delta Plus mass spectrometer. The results were corrected using three laboratory standards (calibrated against international water standards) and are reported using the standard delta notation versus SMOW. Reproducibility was better than 0.1‰ based on repeats of laboratory standards.

Plant predawn xylem water potential measurements where made on freshly clipped fine stems using a Scholander-type pressure bomb. Five oak trees were sampled on each sampling date, and measurements were conducted on three fine stems per tree. Soil water potential measurements were conducted at the lab on freshly collected soil samples using the chilled mirror dewpoint method (CX-2, Decagon Devices, Pullman WA, Gee et al., 1992).

Extramatrical hyphae were extracted from duplicate subsamples of each soil core using a modification of the procedure of Frey and Ellis (1997). For an individual subsample, seven grams of soil were suspended in 200 ml of sodium hexametaphosphate (39.5 g l^{-1}) for 1 h, washed through a 250 μm mesh, re-suspended in 300 ml of distilled water, left to settle for 15 s, and then decanted through a 28 μm mesh. Hyphae were rinsed out of the 28 μm mesh and into 50 ml of distilled water. Duplicate aliquots (each 5 ml) were pipetted after 30 s and each filtered over a 1.2 μm pore membrane. The membranes were mounted on glass slides using a PVA-glycerol-lactic acid-mounting medium, and viewed and scored using a compound microscope ($\times 200$). Fifty random fields of view were scored for hyphae using the gridline intersect method and converted to hyphal length per dry mass soil (Newman, 1966; Tennant, 1975).

Hyphal length values in May and October were compared using a Wilcoxon sign-rank test for paired observations to determine whether soil hyphal abundance

in the 0–200 cm profile declined significantly during the summer drought period in each system.

3. Results

3.1. Soil and plant water potentials

At the start of the dry season, the water potential profile in the grassland showed highly negative values near the surface that steadily increased with depth down to 2 m (Table 2). In contrast, the soil profile in the oak stand showed comparatively less negative water potentials near the surface and a relatively uniform vertical distribution of values (Table 2). The upper part of the soil profile was moister in the oak stand than in the grassland on both sampling dates. The reverse pattern was observed in deeper layers of the soil profile, which were moister in the grassland than in the oak stand at both dates. Soil water potential in the grassland declined sharply over the summer drought period, particularly in upper soil layers (0–40 cm, Table 2). The upper soil horizons in the oak stand showed comparatively less dry down over the same period. Predawn xylem water potential values in oaks were around -0.4 ± 0.1 MPa ($n=5$) at both the early (May) and the late (October) stages of the dry season. Throughout the summer drought period, oaks maintained predawn water potential values which were significantly (Mann–Whitney U-test, $P<0.001$) above those recorded in the 0–200 cm soil depth interval, strongly suggesting root access to groundwater or moist soil layers below 2 m depth.

3.2. Isotopic composition of soil water

Soil samples collected at the end of the dry season plotted to the right of the local meteoric water line (LMWL) in both the grassland and the oak stand (Fig. 1). However, soil water in the upper 40 cm of the profile in the oak stand showed significantly (Mann–Whitney U-Test, $P<0.001$) less enriched δD and $\delta^{18}O$ values that departed less from the LMWL.

3.3. Soil hyphal length

Soil hyphal length in the 0–160 cm depth interval was greater in the oak stand than in the grassland system at both sampling dates (Wilcoxon sign-rank test, $P<0.001$).

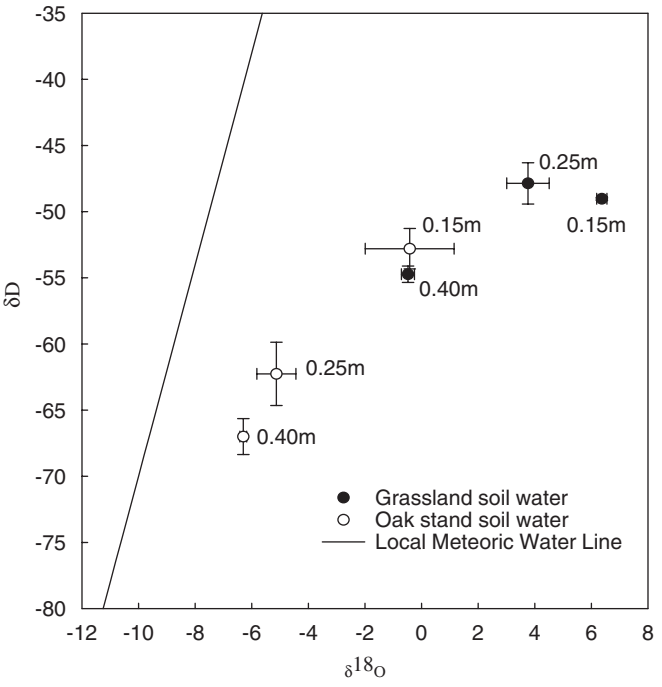

Fig. 1. Local meteoric water line (LMWL; D.P. Rodoni, M. Sci. thesis, Univ. California Riverside, 1993) and hydrogen and oxygen isotopic composition of soil water in the oak stand and the grassland systems in October 2001 (late dry season). Means and standard errors are shown ($n=3$).

Table 2
Vertical distribution of soil water potentials in the oak stand and in the open grassland systems in the early (May) and late (October) dry season in 2001

Soil depth (m)	Soil water potential (MPa) May 2001		Soil water potential (MPa) October 2001	
	Grassland	Oak stand	Grassland	Oak stand
0.05	−37.8±1.1	−4.3±1.9	−149.8±10.6	−20.4±1.9
0.15	−4.0±0.2	−2.1±0.4	−78.8±14.1	−3.6±0.2
0.25	−3.1±0.4	−1.9±0.4	−23.1±2.4	−2.9±0.4
0.40	−2.3±0.3	−1.3±0.1	−7.7±0.7	−2.9±0.2
0.60	−2.3±0.4	−1.4±0.2	−5.0±0.5	−3.0±0.1
0.80	−1.9±0.5	−1.8±0.2	−4.0±0.3	−3.0±0.2
1.00	−1.6±0.2	−1.8±0.2	−3.5±0.5	−3.2±0.3
1.20	−1.1±0.3	−2.0±0.2	−3.0±0.4	−2.9±0.2
1.40	−0.9±0.4	−1.6±0.3	−2.6±0.6	−2.9±0.1
1.60	−0.9±0.4	−1.7±0.1	−1.5±0.2	−2.4±0.2
1.80	−0.7±0.3	−1.5±0.2	−1.0±0.1	−2.0±0.3
2.00	−0.6±0.2	−1.3±0.2	−0.8±0.1	−1.5±0.2

Means±standard errors are shown ($n=3$).

In the upper soil layers (5–40 cm), hyphal length was between twofold and fourfold larger in the oak stand than in the grassland at the start of the dry season. Differences were even larger at the 60–120 cm depth interval, with soil hyphal length values up to 17 times greater in the oak stand than in the grassland in May. These differences increased further during the summer drought, reaching in October hyphal length values that were about 4–12 times higher in the oak stand than in the grassland at the 0–40 cm depth interval. Differences between the two systems peaked at 100–160 cm depth interval, with soil hyphal length values up to 23 times higher in the oak stand than in the grassland in October. Hyphal abundance at 180–200 cm depth was similarly low in the two systems at both sampling dates.

Hyphal length in the soil profile declined markedly in the grassland (Wilcoxon sign-rank test, $P = 0.023$) during the summer drought period (Fig. 2). In the upper soil layers, this decrease ranged between 41% at 5 cm depth and 75% at 40 cm depth. Hyphal abundance in the grassland showed little seasonal fluctuation at the 60–140 cm depth interval, but again tended to decrease between 160 and 200 cm. By contrast, hyphal length in the oak stand decreased only in the shallowest soil layer (49% decrease at 5 cm depth) during the summer drought period. Hyphal length in the rhizosphere of oak trees remained unchanged over most of the vertical soil profile during the 5-month summer drought (Wilcoxon sign-rank test, $P = 0.480$), and even increased at 80 cm depth.

4. Discussion

4.1. Evidence of hydraulic lift

Large differences in soil moisture availability and vertical distribution were found between the oak stand and the adjacent grassland. Direct evaporation of soil water was much more intense and affected deeper layers of the profile in the grassland compared to the oak stand, as indicated by extremely negative water potential values and very enriched isotopic composition of soil water near the surface (Williams and Ehleringer, 2000). While the roots of *Bromus* grasses can reach 1.2 m deep and can extract water at least down to 0.8 m depth (Leffler et al., 2005), transpiration water loss from subsurface soil layers was most likely minimal in the open grassland during the summer because grasses senesced around the time of first

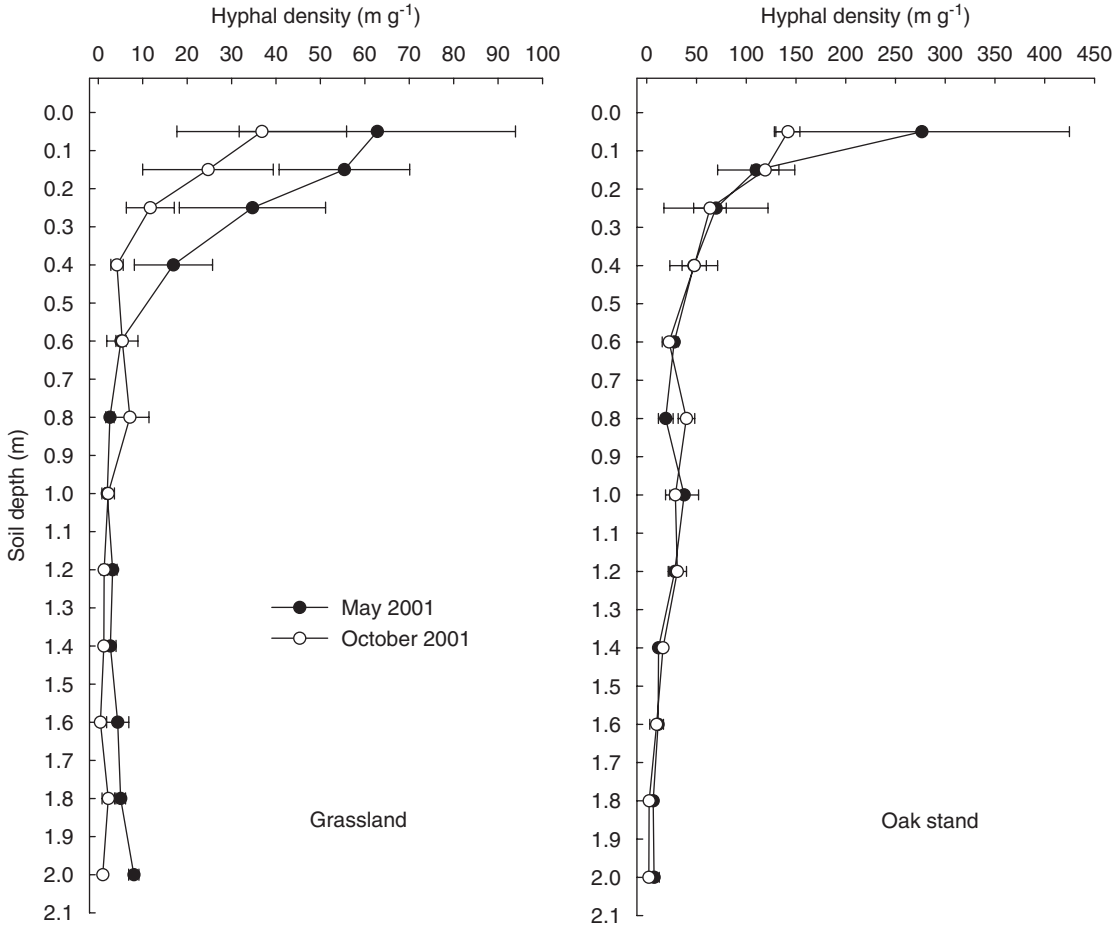

Fig. 2. Hyphal density at different soil depths in the oak stand and the grassland systems at the early and late stages of the summer dry period. Note the different scales on the *x*-axis. Means and standard errors are shown ($n = 3$).

sampling in May. In the oak stand, the remarkably uniform vertical distribution of soil water potential values suggested homogeneous utilization of moisture stored in the profile by coast live oaks. Soil below 120–160 cm depth showed more negative water potential values in the oak stand than in the adjacent grassland at both sampling dates, indicating deep moisture depletion by tree roots. The higher water potentials and more negative water isotopic values in near-surface soil in the oak stand than in the adjacent grassland could be explained in part by canopy shading effects in the former during the long summer drought period. The presence of a tree canopy in semiarid ecosystems generally lowers soil temperatures and increases relative humidity (Kennedy and Sousa, 2006), thus reducing both the direct evaporation from the soil surface, and evaporative isotopic enrichment of soil water (Barnes and Turner, 1998).

Considering the length and severity of drought, subsurface (15–40 cm) soil water potential values in the oak stand decreased little between May and October despite a high transpiration demand by oak trees. Lifting of groundwater or deep soil water and efflux by oak roots could explain this relatively small decline in subsurface soil water potentials over the long summer drought period. Plants conducting hydraulic lift typically show slowly decreasing water potentials in their rhizosphere soil during prolonged dry periods (Caldwell et al., 1998). Less isotopically enriched soil water at the 15–40 cm depth interval in the oak stand compared to the grassland in October could also be attributable to root exudation of isotopically depleted groundwater or deep soil water not exposed to evaporation. Higher soil water potential and more isotopically depleted soil water in the rhizosphere of deep-rooted trees compared to surrounding soil has been taken as evidence of hydraulic lift (Dawson, 1993). Throughout the entire summer drought period, soil water potentials at the 15–40 cm depth interval in the oak stand remained well above the minimum threshold at which hydraulic lift has been recorded for California oaks (−4.5 MPa, Ishikawa and Bledsoe, 2000; −4.2 MPa, Querejeta et al., 2003), which further supports our interpretation of the data. Taproot access to groundwater, as well as large soil water potential gradients over the range of depth spanned by oak roots (both strongly supported by predawn xylem water potentials), likely favoured the persistence of hydraulic redistribution in the oak stand until late into the dry season. Although the roots of senescent *Bromus* grasses have been reported to conduct hydraulic lift (Leffler et al., 2005), the isotopic and water potential data collected in late dry season in this study showed no evidence of hydraulic redistribution within the grassland.

4.2. Changes in soil hyphal length

Hyphal abundance in upper soil layers of the grassland (Fig. 2) fell well within the range of values reported for other temperate grasslands (Lutgen et al., 2003 and references therein), while hyphal length in the oak stand was at the lower range of published values for forests ecosystems in temperate latitudes (Hunt and Fogel, 1983 and references therein). Soil hyphal length declined with depth in both the oak stand and the grassland (Fig. 2), as previously noted by many other studies (Berg et al., 1998; Hunt and Fogel, 1983; Wallander et al., 2004). Both mycorrhizal and saprophytic fungi tend to concentrate in upper soil horizons where nutrients and organic matter are most abundant (Hunt and Fogel, 1983). However it is interesting to note that hyphal length values were rather high at the 80–160 cm depth interval in the oak stand at both sampling dates, which supports Bornyasz et al. (2005) suggestion that deep nutrient and water uptake by mycorrhizal mycelium could be important for coast live oaks growing under semiarid conditions in Southern California.

The large summer decrease in soil hyphal length observed in the AM-dominated grassland was anticipated, since grass senescence at the start of the dry season deprived AM mycelia of their major carbon source. Moreover, upper soil layers in the grassland underwent extreme desiccation during the summer, which most likely exerted a direct negative effect on hyphae (Augé, 2001; McMillen et al., 1998; Braunberger et al., 1996). The rate of decomposition of soil hyphae within the exceedingly dry upper soil layers of the AM-dominated grassland (41–75% decline in hyphal length from May until October) was strikingly similar to that measured by Steinberg and Rillig (2003) in a Montana grassland (where 60% of soil hyphal length decomposed in 150 days). This suggests that the turnover rate of soil hyphae in AM dominated grasslands might show very little variation across different ecosystems.

Soil hyphal length in the oak stand remained remarkably constant throughout the summer drought period, with the only exception of the topsoil layer exposed to direct evaporation (5 cm depth). These results are in sharp contrast to those obtained by Hunt and Fogel (1983), who found that soil hyphal length at 10–50 cm depth in an EM-dominated Douglas-fir forest in Oregon decreased between two- and fourfold during the summer dry period. Other studies have also shown that soil hyphal biomass in forest ecosystems is positively correlated with soil moisture levels, so that hyphal abundance declines during drought periods (Berg et al., 1998; Osono et al., 2003). The lack of response of soil hyphal length to extreme meteorological drought in the oak stand could be explained in part by the fact that oaks remained well hydrated during the summer as a result of access to groundwater, and thus continued supplying carbon to their mycorrhizal fungi. Consequently, any negative impacts of drought on soil hyphal abundance reported previously may largely reflect the effects of host plant carbon balance. However, the 49% summer decrease in hyphal length in the uppermost soil layer (5 cm) of the oak stand strongly supports a direct negative effect of severe soil drying on rhizosphere hyphae (McMillen et al., 1998; Augé, 2001; Sánchez et al., 2001; Duñabeitia et al., 2004; Izzo et al., 2005).

The sustained exudation of water from roots to soil through hydraulic redistribution may have buffered rhizosphere hyphae at the 15–40 cm depth interval against the negative effects of extreme soil desiccation in the oak stand, thus preventing hyphal senescence as was suggested by Caldwell et al. (1998). Pure cultures of some drought resistant California EM fungi have been shown to be capable of growing at water potentials of −3 MPa (Coleman et al., 1989), which is similar to the soil water potentials maintained at 15–200 cm in the oak stand during the summer. Mycorrhizal fungi might be able to continue growth at even more negative soil water potentials than that when they are in intimate association with a host plant that is well hydrated because of deep root access to groundwater. Direct transfer of water from well hydrated, deep rooted oaks to mycorrhizae can contribute to prolong the lifespan of both EM and AM extraradical hyphae in dry soil, and could support the production of new hyphae (Querejeta et al., 2003). However water efflux from roots to soil and direct water transfer from plant to extraradical mycorrhizal hyphae may have not been sufficient to compensate for evaporation losses at 5 cm depth in the oak stand. Death of surface fine roots in response to severe drying of the topsoil may function as a hydraulic fuse that prevents excessive water efflux into the soil (Espeleta et al., 2004). This may have led to the senescence of extraradical mycorrhizal hyphae associated to those fine roots in the topsoil of the oak stand.

Saprophytic hyphae are generally indistinguishable from EM hyphae based on morphological traits, so we cannot rule out the possibility that a significant proportion of soil hyphae in the oak stand were saprophytic. For example, Wallander et al. (2004) estimated that 20–50% of soil hyphae at the 0–70 cm depth interval were saprophytes in an EM dominated oak-spruce forest in Sweden. Saprophytic fungi often proliferate on dead or decaying external mycorrhizal mycelium (Colpaert and van Assche, 1993). However, a major summer shift in the functional group composition of the soil fungal community from mycorrhizal to saprophytic in the oak stand seems unlikely, since oaks were well buffered from meteorological drought because of host root access to groundwater, and presumably continued supplying carbon to their mycorrhizal symbionts. Further, soil at the 15–200 depth interval in the oak woodland maintained until late into the dry season water potentials values that many native EM fungi can tolerate well (Coleman et al., 1989).

The only plausible explanations for the persistence of high soil hyphal length values in the oak stand until late into the dry season were either the preservation of the integrity of fungal mycelia throughout the summer, or the continued production of new hyphae to replace decaying hyphae, or both. Given the short lifespan and high turnover rate of hyphae, it seems unlikely that the standing biomass of hyphae at 15–200 cm depth in the oak stand could have remained stable through 5 months of drought without the concurring production of new hyphae. Our data suggest that hydraulic lift by deep-rooted trees could influence the biogeochemical cycling of carbon and nutrients in semiarid ecosystems through effects on rhizosphere fungi. By extending the lifespan and supporting the growth of both mycorrhizal and saprophytic hyphae in dry upper soil layers, hydraulic lift could favour the stability and persistence of the fungal carbon pool in plant rhizosphere during prolonged drought periods, which has implications for soil carbon storage and for soil aggregation (Fogel and Hunt, 1979; Treseder and Allen, 2000; Rillig, 2004). Hydraulic lift could also reduce mineralization rates by favouring nutrient immobilization in fungal tissue during the summer drought period (Fogel and Hunt, 1983; Entry et al., 1992; Pampolina et al., 2002; Treseder et al., 2005), thus minimizing subsequent leaching losses from upper soil layers at the onset of the following rainy season in the fall. Finally, coast live oaks supporting a high standing biomass of extraradical mycorrhizal hyphae during drought could be able to simultaneously exploit two spatially discrete resource pools, namely nutrients in upper soil layers and water stored at depth (Querejeta et al., 2003).

5. Conclusions

Soil hyphal length in the rhizosphere of well-hydrated coast live oaks accessing groundwater and conducting hydraulic lift was to a large extent decoupled from current precipitation in a Mediterranean oak savanna in Southern California. In contrast to previous studies reporting sharp declines in mycelial abundance during drought in forest ecosystems elsewhere, hyphal length values in most of the soil profile (15–200 cm depth) of the oak stand remained stable throughout the prolonged summer dry period. Soil hyphal length in the adjacent grassland declined markedly during the summer, indicating rapid turnover of the AM dominated hyphal carbon pool under extreme drought. Further studies in different ecosystems will be needed to determine whether the persistence of high soil hyphal abundance values during drought in the rhizosphere of deep rooted trees conducting hydraulic lift is a widespread phenomenon in seasonally dry environments.

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References

Allen, M.F., Klironomos, J.N., Treseder, K.K., Oechel, W.C., 2005. Responses of soil biota to elevated CO_2 in a chaparral ecosystem. Ecological Applications 15, 1710–1711.

Augé, R.M., 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. Mycorrhiza 11, 3–42.

Bååth, E., Nilsson, L.O., Goransson, H., Wallander, H., 2004. Can the extent of degradation of soil fungal mycelium during soil incubation be used to estimate ectomycorrhizal biomass in soil? Soil Biology & Biochemistry 36, 2105–2109.

Barnes, C.J., Turner, J.V., 1998. Isotopic exchange in soil water. In: Kendall, C., McDonnell, J.J. (Eds.), Isotope Tracers in Catchment Hydrology. Elsevier, Amsterdam, The Netherlands.

Berg, M.P., Kniese, J.P., Verhoef, H.A., 1998. Dynamics and stratification of bacteria and fungi in the organic layers of a Scots pine forest soil. Biology & Fertility of Soils 26, 313–322.

Bornyasz, M.A., Graham, R.C., Allen, M.F., 2005. Ectomycorrhizae in a soil-weathered granitic bedrock regolith: linking matrix resources to plants. Geoderma 126, 141–160.

Braunberger, P.G., Abbott, L.K., Robson, A.D., 1996. Infectivity of arbuscular mycorrhizal fungi after wetting and drying. New Phytologist 134, 673–684.

Caldwell, M.M., Dawson, T.E., Richards, J.H., 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113, 151–161.

Coleman, M.D., Bledsoe, C.S., Lopushinsky, W., 1989. Pure culture response of ectomycorrhizal fungi to imposed water stress. Canadian Journal of Botany 67, 29–39.

Colpaert, J.V., van Assche, J.A., 1993. The effects of cadmium on ectomycorrhizal *Pinus sylvestris* L. New Phytologist 123, 325–333.

Dawson, T.E., 1993. Hydraulic lift and water use by plants: implications for water-balance, performance and plant–plant interactions. Oecologia 95, 565–574.

Duñabeitia, M.K., Hormilla, S., García-Plazaola, J.I., Txarterina, K., Arteche, U., Becerril, J.M., 2004. Differential responses of three fungal species to environmental factors and their role in the mycorrhization of *Pinus radiata* D. Don. Mycorrhiza 14, 11–18.

Egerton-Warburton, L.M., Allen, M.F., 2001. Endo- and ectomycorrhizas in *Quercus agrifolia* Nee. (Fagaceae): patterns of root colonization and effects on seedling growth. Mycorrhiza 11, 283–290.

Egerton-Warburton, L.M., Graham, R.C., Hubbert, K.R., 2003. Spatial variability in mycorrhizal hyphae and nutrient and water availability in a soil-weathered bedrock profile. Plant & Soil 249, 331–342.

Ehleringer, J.R., Osmond, C.B., 1989. Stable isotopes. In: Pearcy, R.W., Ehleringer, J.R., Mooney, H.A., Rundel, P.W. (Eds.), Plant Physiological Ecology: Field Methods and Instrumentation. Chapman & Hall, New York, USA.

Entry, J.A., Rose, C.L., Cromack, K., 1992. Microbial biomass and nutrient concentrations in hyphal mats of the ectomycorrhizal fungus *Hysterangium setcellii* in a coniferous forest soil. Soil Biology & Biochemistry 24, 447–453.

Espeleta, J.F., West, J.B., Donovan, L.A., 2004. Species-specific patterns of hydraulic lift in co-occurring adult trees and grasses in a sandhill community. Oecologia 138, 341–349.

Fogel, R., Hunt, G., 1979. Fungal and arboreal biomass in a Western Oregon Douglas-fir ecosystem: distribution patterns and turnover. Canadian Journal of Forest Research 9, 245–256.

Fogel, R., Hunt, G., 1983. Contribution of mycorrhizae and soil fungi to nutrient cycling in a Douglas-fir ecosystem. Canadian Journal of Forest Research 13, 219–232.

Frey, J.E., Ellis, J.R., 1997. Relationship of soil properties and soil amendments to response of *Glomus intraradices* and soybeans. Canadian Journal of Botany 75, 483–491.

Frey, S.D., Elliott, E.T., Paustian, K., 1999. Bacterial and fungal abundance and biomass in conventional and non-tillage agroecosystems along two climatic gradients. Soil Biology & Biochemistry 31, 573–585.

Friese, C.F., Allen, M.F., 1991. The spread of VA mycorrhizal fungal hyphae in the soil: inoculum types and external hyphal architecture. Mycologia 83, 409–418.

Gee, G.W., Campbell, M.D., Campbell, G.S., Campbell, J.H., 1992. Rapid measurement of low soil water potentials using a water activity meter. Soil Science Society of America Journal 56, 1068–1070.

Hunt, G.A., Fogel, R., 1983. Fungal hyphal dynamics in a Western Oregon Douglas-fir stand. Soil Biology & Biochemistry 15, 641–649.

Ishikawa, C.M., Bledsoe, C.S., 2000. Seasonal and diurnal patterns of soil water potential in the rhizosphere of blue oaks: evidence for hydraulic lift. Oecologia 125, 459–465.

Izzo, A., Agbowo, J., Bruns, T.D., 2005. Detection of plot-level changes in ectomycorrhizal communities across years in an old-growth mixed-conifer forest. New Phytologist 166, 619–630.

Juniper, S., Abbott, L., 1993. Vesicular-arbuscular mycorrhizas and soil salinity. Mycorrhiza 4, 45–57.

Kaneda, S., Kaneko, N., 2004. The feeding preference of a collembolan (*Folsomia candida* Willem) on ectomycorrhiza (*Pisolithus tinctorius* (Pers.)) varies with mycelial growth condition and vitality. Applied Soil Ecology 27, 1–5.

Kennedy, P.G., Sousa, W.P., 2006. Forest encroachment into a California grassland: examining the simultaneous effects of facilitation and competition on tree seedling recruitment. Oecologia.

Langley, J.A., Hungate, B.A., 2003. Mycorrhizal controls on belowground litter quality. Ecology 84, 2302–2312.

Leffler, A.J., Peek, M.S., Ryel, R.J., Ivans, C.Y., Caldwell, M.M., 2005. Hydraulic redistribution through the root systems of senesced plants. Ecology 86, 633–642.

Li, L.F., Yang, A., Zhao, Z.W., 2005. Seasonality of arbuscular mycorrhizal symbiosis and dark septate endophytes in a grass land site in southwest China. FEMS Microbiology Ecology 54, 367–373.

Lutgen, E.R., Muir-Clairmont, D., Graham, J., Rillig, M.C., 2003. Seasonality of arbuscular mycorrhizal hyphae and glomalin in a western Montana grassland. Plant & Soil 257, 1–71.

McMillen, B.G., Juniper, S., Abbott, L.K., 1998. Inhibition of hyphal growth of a vesicular-arbuscular mycorrhizal fungus in soil containing sodium chloride limits the spread of infection from spores. Soil Biology & Biochemistry 30, 1639–1646.

Morris, S.J., Boerner, R.E.J., 1999. Spatial distribution of fungal and bacterial biomass in southern Ohio hardwood forest soils: scale dependency and landscape patterns. Soil Biology & Biochemistry 31, 887–902.

Newman, E.I., 1966. A method of estimating the total length of a root sample. Journal of Applied Ecology 3, 139–145.

Osono, T., Ono, Y., Takeda, H., 2003. Fungal ingrowth on forest floor and decomposing needle litter of *Chamaecyparis obtusa* in relation to resource availability and moisture condition. Soil Biology & Biochemistry 35, 1423–1431.

Pampolina, N.M., Dell, B., Malajczuk, N., 2002. Dynamics of ectomycorrhizal fungi in an *Eucalyptus globulus* plantation: effects of phosphorus fertilization. Forest Ecology & Management 158, 291–304.

Querejeta, J.I., Egerton-Warburton, L.M., Allen, M.F., 2003. Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. Oecologia 134, 55–64.

Rillig, M.C., 2004. Arbuscular mycorrhizae and terrestrial ecosystem processes. Ecology Letters 7, 740–754.

Sánchez, F., Honrubia, M., Torres, P., 2001. Effects of pH, water stress and temperature on in vitro cultures of ectomycorrhizal fungi from Mediterranean forests. Criptogamie Mycologie 22, 243–258.

Sharp, Z.D., Atudorei, V., Durakiewicz, T., 2001. A rapid method for determination of hydrogen and oxygen isotope ratios from water and hydrous minerals. Chemical Geology 178, 197–210.

Staddon, P.L., Ramsey, C.B., Ostle, N., Ineson, P., Fitter, A.H., 2003a. Rapid turnover of hyphae of mycorrhizal fungi determined by AMS microanalysis of C-14. Science 300, 1138–1140.

Staddon, P.L., Thompson, K., Jakobsen, I., Grime, J.P., Askew, A.P., Fitter, A.H., 2003b. Mycorrhizal fungal abundance is affected by long-term climatic manipulations in the field. Global Change Biology 9, 186–194.

Steinberg, P.D., Rillig, M.C., 2003. Differential decomposition of arbuscular mycorrhizal fungal hyphae and glomalin. Soil Biology & Biochemistry 35, 191–194.

Tennant, D., 1975. A test of the modified root intersect method of estimating root length. Journal of Ecology 63, 995–1001.

Treseder, K.K., Allen, M.F., 2000. Mycorrhizal fungi have a potential role in soil carbon storage under elevated CO_2 and nitrogen deposition. New Phytologist 147, 189–200.

Treseder, K.K., Allen, M.F., Ruess, R.W., Pregitzer, K.S., Hendrick, R.L., 2005. Lifespans of fungal rhizomorphs under nitrogen fertilization in a pinyon-juniper woodland. Plant & Soil 270, 249–255.

Wallander, H., Goranson, H., Rosengren, U., 2004. Production, standing biomass and natural abundance of N-15 and C-13 in ectomycorrhizal mycelia collected at different soil depths in two forest types. Oecologia 139, 89–97.

Williams, D.G., Ehleringer, J.R., 2000. Intra- and interspecific variation for summer precipitation use in pinyon-juniper woodlands. Ecological Monographs 70, 517–537.