The role of hydraulic lift during the establishment of *Quercus agrifolia* seedlings at the Shipley-Skinner Reserve.

Final report of the proposal submitted by Jose I. Querejeta and Michael F. Allen to the UCR faculty-Shipley Skinner Reserve

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Introduction

Due to extreme drought conditions during 2002, it would have been impractical to carry out an experimental planting of oak seedlings in the field as planned in the original research proposal. Precipitation during the January-May period (32 mm) was 86% below normal (220 mm, 30 year average) in 2002. Given the focus of this study on water relations, watering the seedlings to prevent massive mortality would have rendered the results of the experiment meaningless, and was not an option.

In order to circumvent this unexpected problem, an alternative approach was chosen. We identified and compared two neighboring locations in Lopez Canyon which show contrasting levels of natural oak seedling regeneration. The mesic valley location shows abundant seedling establishment and survival, while no seedling regeneration can be found at the more xeric hill location. Seedling regeneration within the oak stand at the valley site shows a patchy distribution, with highest density of seedlings under the canopy of adult trees. Most of these oak seedlings around mature trees in the valley site were able to survive the intense drought of 2002. Up to 15 oak seedlings per square meter were present under the canopy of some mature individuals throughout the drought period. Previous studies have shown that adult trees in the valley bottom site have access to a relatively shallow aquifer (3-5 m deep), while trees in the hill site don't. Accordingly, adult trees in the hill site show increasingly negative predawn xylem water potentials during the long rainless summer period (down to -2.2 MPa in October 2000), whereas mature oaks in the valley bottom site maintain similarly high predawn water potentials all year round (-0.3 MPa).

The clustered distribution of oak seedlings around mature trees in the valley oak stand suggests that the redistribution of groundwater to the upper soil by the root of mature oaks (hydraulic lift) may represent an important facilitation mechanism favoring seedling establishment and survival during drought. Moreover, this process has been shown to maintain the integrity and functionality of the mycorrhizal symbiosis in very dry upper soil layers, which may also favor seedling regeneration around adult trees. We hypothesized that adult trees in the valley site conduct extensive hydraulic lift during drought periods thanks to access to groundwater, thus maintaining higher levels of soil moisture and a well developed and functional mycorrhizal matrix in their rhizosphere. These facilitation mechanisms could explain the patchy distribution of seedlings observed in the field, and have important implications for ecosystem restoration and for the long term management of *Quercus agrifolia* woodlands in semiarid Southern California.

Methods

In May 2002, soil cores (8 cm diameter, 0-50 cm deep) were collected in the rhizosphere of ten mature oak trees (5 in the valley site, 5 in the hill site) using a hand auger. All soil samples were collected under the oak canopy within 2 m of the tree trunk. Soil water potential and the hydrogen isotopic composition of soil water were measured at 10 cm depth intervals. Oak roots in each soil core were handpicked and their mycorrhizal status was evaluated. Ectomycorrhizal (EM) roots were morphotyped, and the percentage EM colonization of the roots was assessed. The diversity and taxonomic composition of the EM fungal community both in the roots and in the soil (extraradical mycelium) was determined using molecular techniques (RFLP and DNA sequencing). Percentage colonization of roots by arbuscular mycorrhizae (AM) was also measured, and the composition of the AM fungal community in oak rhizosphere was determined using inmunofluorescence methods.

Results and discussion

Oak rhizosphere soil was much drier in the hill than in the valley sites in May 2002 (Fig. 1). This difference was even larger when comparing the uppermost soil layers (0-30 cm deep). Higher soil moisture and water potential values which are relatively uniform with depth provide evidence of extensive hydraulic redistribution in the rhizosphere of the valley trees with access to the aquifer.

In contrast, the hydrogen isotopic composition of soil water was very similar in hill and valley sites at all depths (Fig. 2). This suggests that differences in soil moisture were not due to higher soil water evaporation at the more exposed hill locations. Higher soil water evaporation in the hill sites would have resulted in differentially enriched isotopic values in the uppermost layers of the soil profile, but this was not the case. Therefore, differential shading effects cannot account for the very large difference in soil moisture found between the two locations, which further supports the alternative interpretation of extensive hydraulic redistribution in the valley but not in the hill sites.

The percentage EM colonization of the oak roots was much higher in the mesic valley sites than in the xeric hill sites at all soil depths (Fig. 3). The total length of viable extraradical EM hyphae in the rhizosphere soil was also much higher in the valley than in the hill (Fig. 4). Conversely, the level of AM colonization of roots was significantly higher in the hill trees, especially in the uppermost soil layers (Fig. 3).

The composition of the EM fungal community was very different in the two locations. The richness of EM fungal community was much higher in the rhizosphere of the valley oaks (12-17 different genuses found) than in the hill (Fig. 5 and 6). Valley oaks showed a diverse array of EM symbionts. *Russula, Cenococcum, Cortinarius, Lactarius and Pisolithus* were among the most abundant fungal taxa found on the valley oak roots. However, the extraradical phase was dominated by *Boletus, Cortinarius, Rhizopogon, Tomentella* and several unknown *Ascomycetes,* suggesting that dominance on the roots does not necessarily translate into dominance of the extraradical phase.

The EM community in the rhizosphere of the hill trees was integrated by a smaller number of fungal taxa (4-5 genuses). The dominant fungi in the hill site were *Cenococcum, Russula, Cortinarius* and *Boletus.*

The composition of the AM fungal community differed between hill an valley locations (Fig. 7). The most abundant AM fungi in the rhizosphere of the hill oaks were *Glomus* an *Acaulospora,* whereas *Scutellospora* was dominant in the more mesic valley sites.

Our results show that access to groundwater and hydraulic lift allow the mature valley oaks to keep the upper rhizosphere soil relatively moist even during extreme drought. Hydraulic lift and direct transfer of water from plant to fungus prevent the senescence of EM root tips and extraradical mycelium during dry periods, thus maintaining the diversity, integrity and functionality of the EM symbiosis irrespective of current precipitation. Thanks to access to groundwater, valley oaks are probably able to maintain a favorable carbon budget, and mycorrhizae continue receiving an adequate supply of photosynthates from host trees throughout drought periods. The rhizosphere of the valley oaks therefore provide favorable conditions for the establishment and survival of seedlings, buffering them from extreme drought events. In contrast, adult trees in the hill don't have access to groundwater and become progressively more water stressed during prolonged drought. Most of the EM roots and the extraradical mycelium senesce as the upper soil layers reach extremely low water potential values. Since AM fungi are better adapted than EM fungi to xeric conditions, a shift occurs in the composition of the rhizosphere fungal community, with AM species becoming dominant. Very dry soil, a senescent EM mycelial matrix and a fungal community dominated by *Glomus* make the rhizosphere of the hill trees an unsuitable environment for the establishment and survival of oak seedlings.

We conclude that the rhizospheres of mature trees conducting hydraulic lift in mesic valley oak stands provide the only suitable refugia for oak seedlings during drought. Seedlings regeneration in more xeric units of the landscape (hill oak stands, open grasslands) is probably restricted to exceptionally moist years in this water-limited environment.

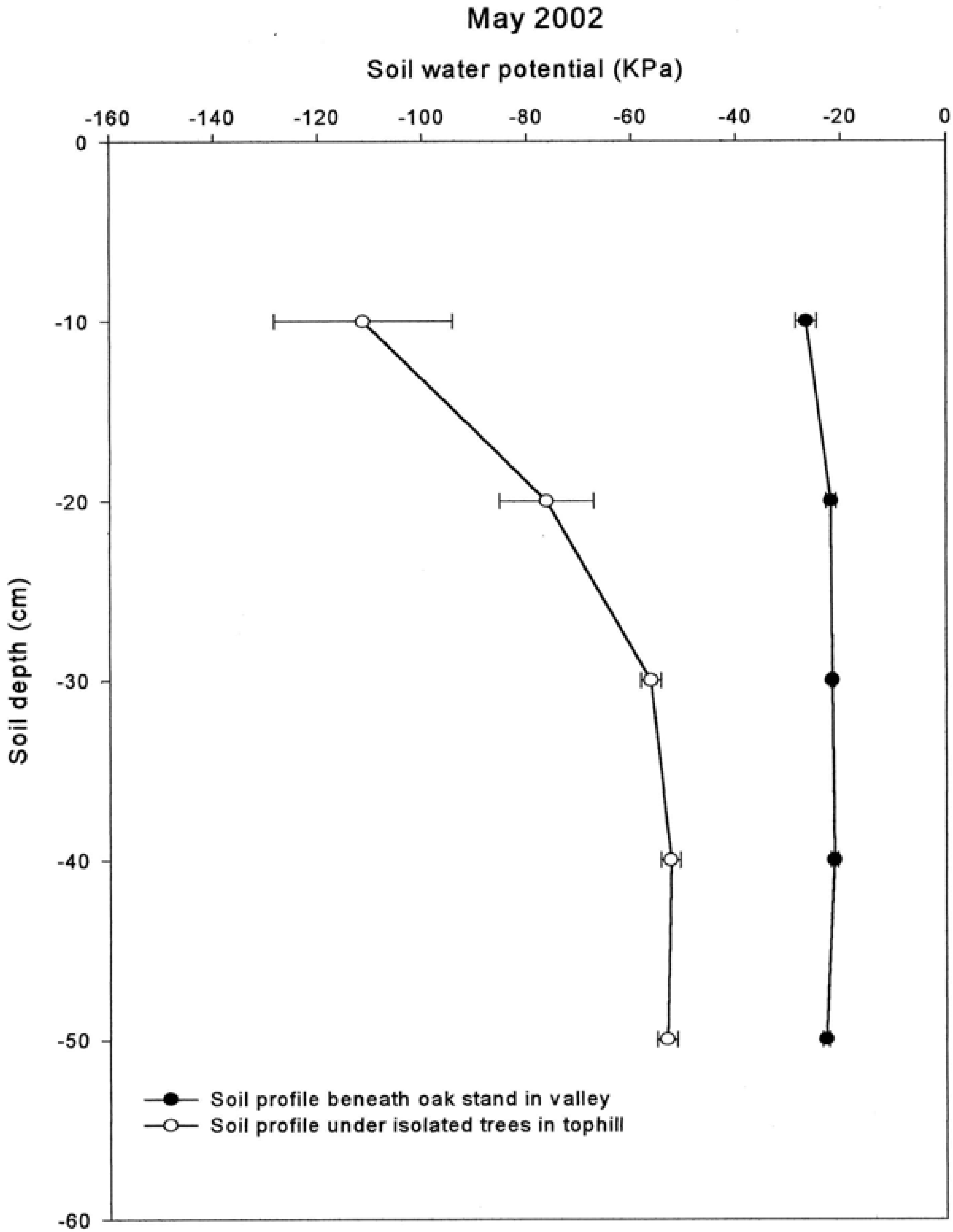

May 2002
Soil water potential (KPa)
-160
-140
-120
-100
-80
-60
-40
-20
0
Soil depth (cm)
0
-10
-20
-30
-40
-50
-60
Soil profile beneath oak stand in valley
Soil profile under isolated trees in tophill

Figure 1

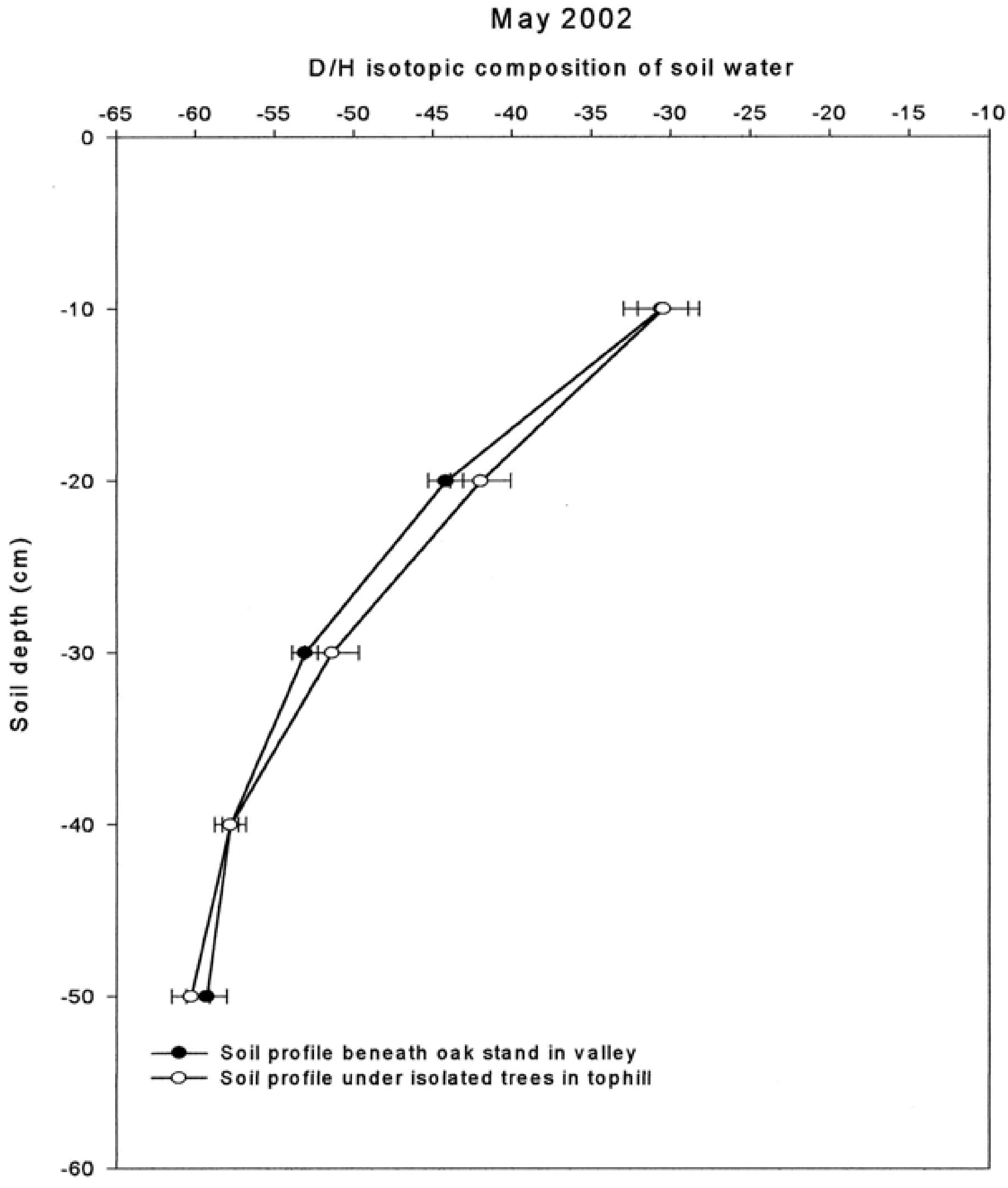

May 2002
D/H isotopic composition of soil water
-65
-60
-55
-50
-45
-40
-35
-30
-25
-20
-15
-10
0
-10
-20
-30
-40
-50
-60
Soil depth (cm)
Soil profile beneath oak stand in valley
Soil profile under isolated trees in tophill

Figure 2

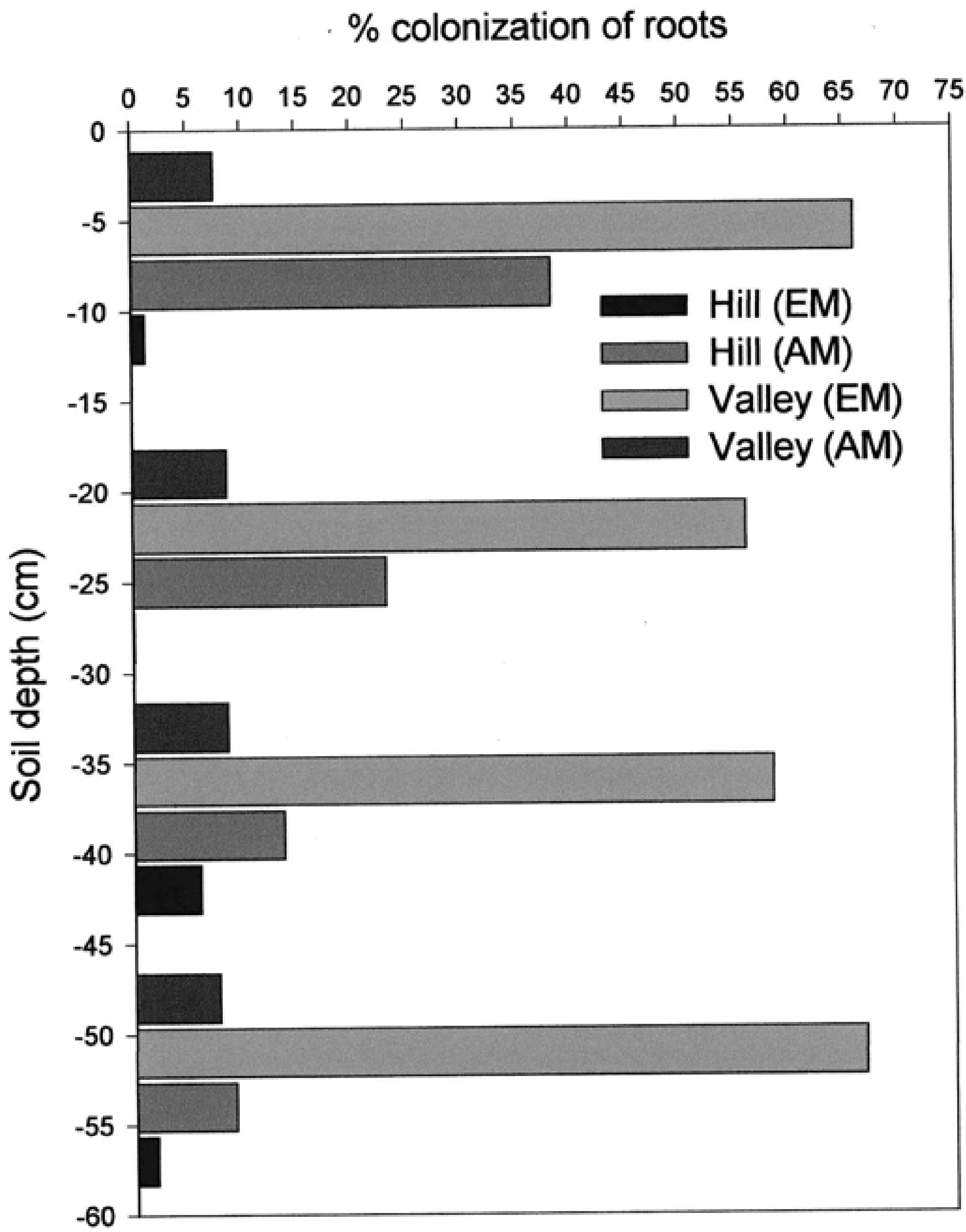
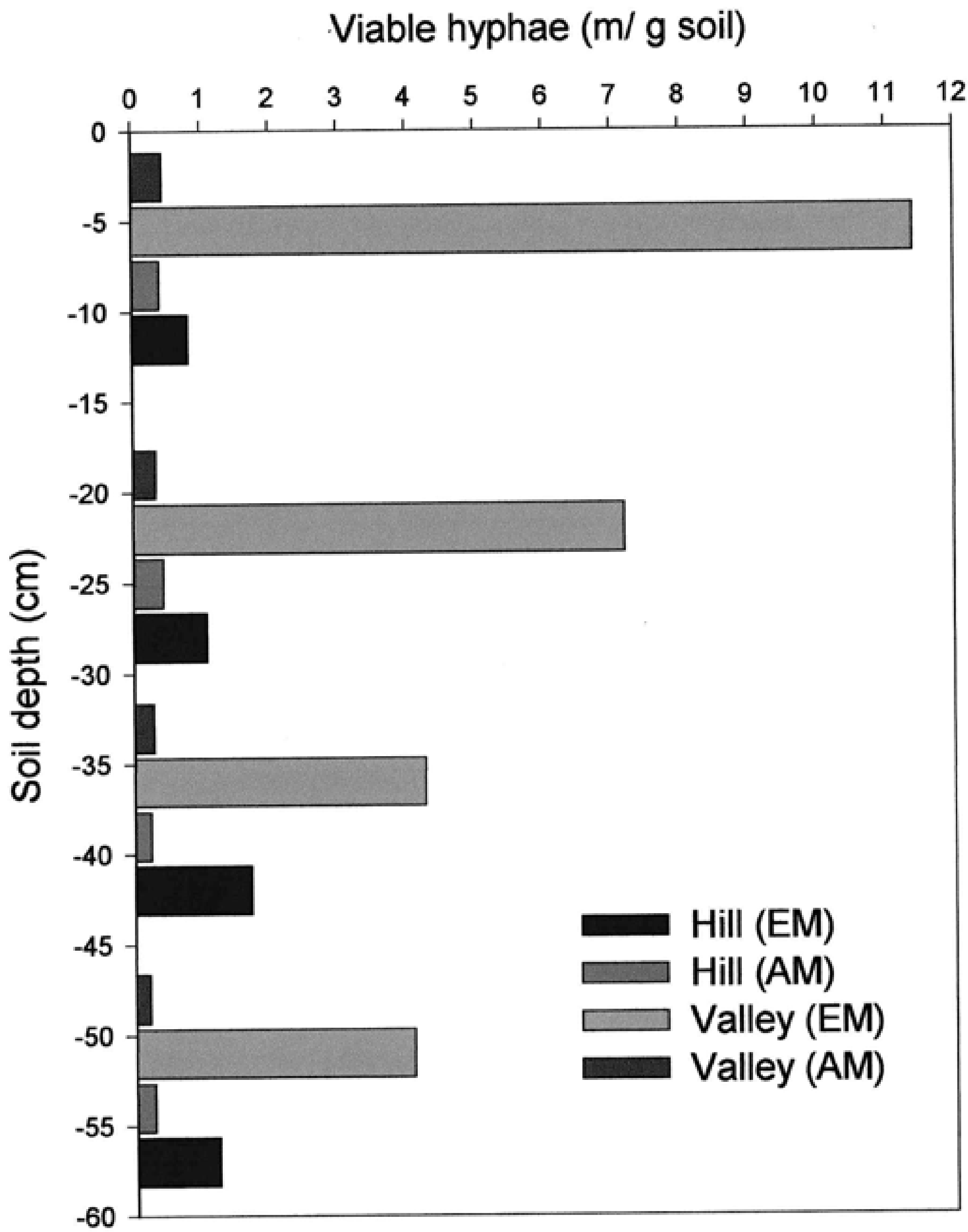
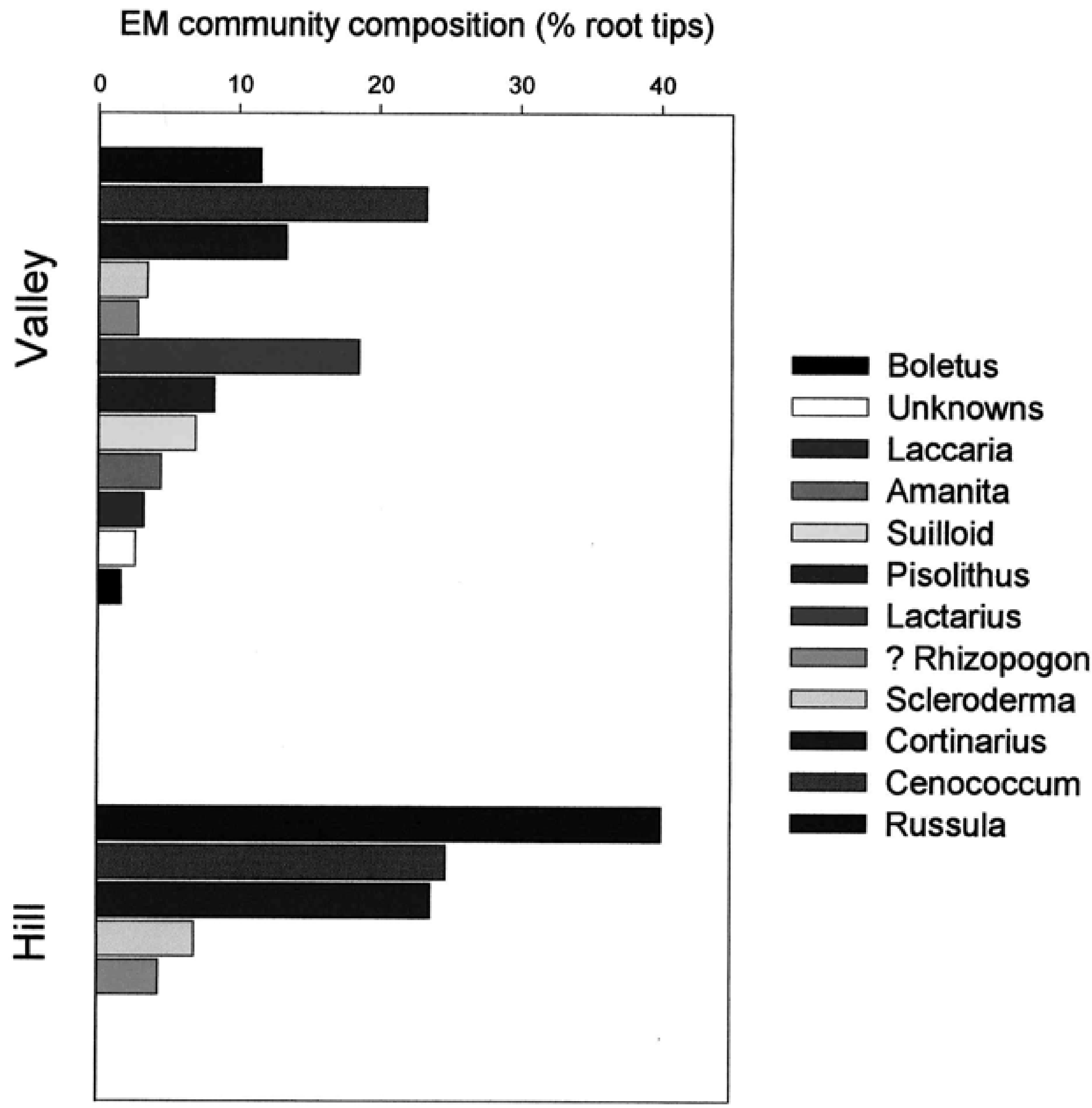

% colonization of roots
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
0
-5
-10
-15
-20
-25
-30
-35
-40
-45
-50
-55
-60
Soil depth (cm)
Hill (EM)
Hill (AM)
Valley (EM)
Valley (AM)

Figure 3



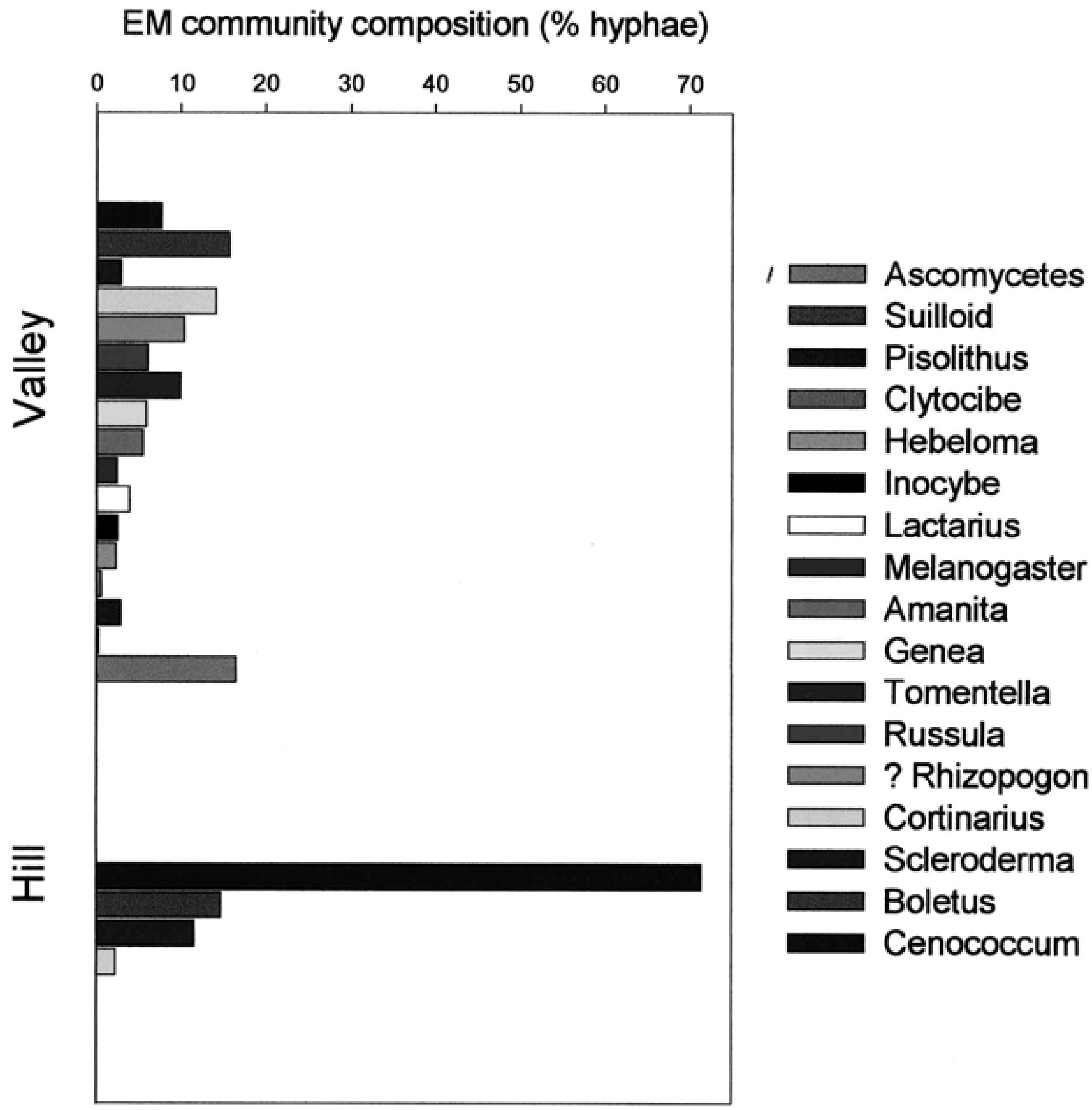
Viable hyphae (m/ g soil)
0
1
2
3
4
5
6
7
8
9
10
11
12
0
-5
-10
-15
-20
-25
-30
-35
-40
-45
-50
-55
-60
Soil depth (cm)
Hill (EM)
Hill (AM)
Valley (EM)
Valley (AM)

Figure 4



EM community composition (% root tips)
0
10
20
30
40
Valley
Hill
Boletus
Unknowns
Laccaria
Amanita
Suilloid
Pisolithus
Lactarius
? Rhizopogon
Scleroderma
Cortinarius
Cenococcum
Russula

Figure 5



EM community composition (% hyphae)
0
10
20
30
40
50
60
70
Valley
Hill
Ascomycetes
Suilloid
Pisolithus
Clytocibe
Hebeloma
Inocybe
Lactarius
Melanogaster
Amanita
Genea
Tomentella
Russula
? Rhizopogon
Cortinarius
Scleroderma
Boletus
Cenococcum

Figure 6

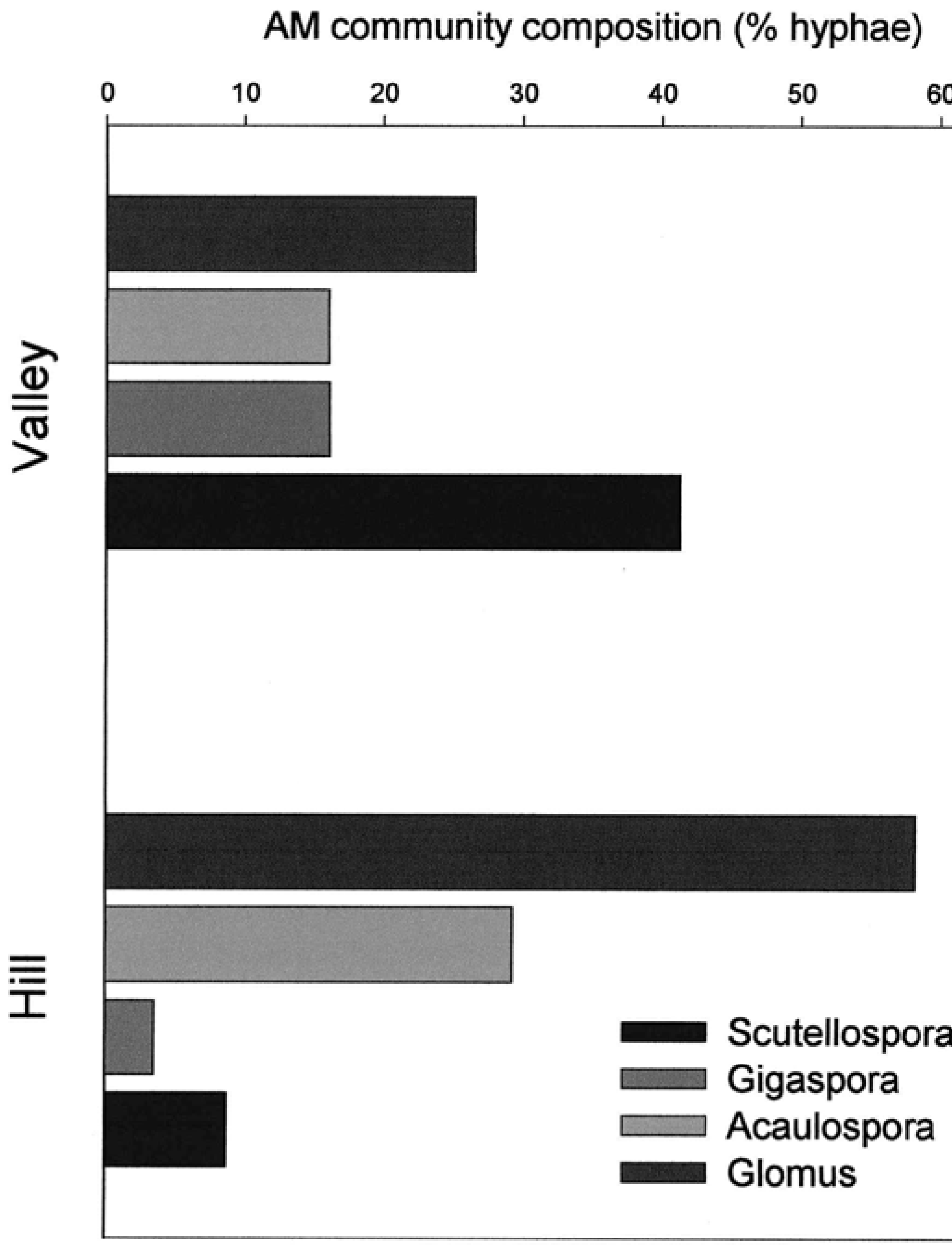

AM community composition (% hyphae)
0
10
20
30
40
50
60
70
Valley
Hill
Scutellospora
Gigaspora
Acaulospora
Glomus

Figure 7