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Alleviation of drought stress of young peach (*Prunus persica* L.) trees by using arbuscular mycorrhizal fungi

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ABSTRACT

It is well known that arbuscular mycorrhizal fungi have favorable effects on nutrients uptake and water relations of plants. On this basis, an experiment was carried out under field conditions to evaluate the effect of arbuscular mycorrhization, realized by a mixture of two mycorrhizal fungi strains, *Glomus intraradices* and *Glomus mosseae*, on drought tolerance of young peach trees. The experiment was performed on four mycorrhizal and non-mycorrhizal peach varieties, one year old, submitted to two water regimes, 50% and 100% ETc. Results showed that young peach trees, even mycorrhized, did not tolerate water stress applied. However, plants were dependent on mycorrhizae under water stress, partially compensating its effects. The compensatory effect of mycorrhizae was related to an increase of water potential and stomatal conductance without changing relative water content of plants. Mycorrhizae also induced a significant increase of phosphorus uptake under water stress. In conclusion, it was demonstrated that arbuscular mycorrhizae significantly improve water and nutrient use efficiency of young peach trees submitted to water stress of 50% ETc. The observed improvements due to mycorrhizae were considerable, suggesting possibility of adoption of this water restriction to optimize deficit irrigation of mycorrhizal plants of this rosacea under low water availability conditions.

KEYWORDS

Prunus persica;
Water stress;
Arbuscular mycorrhizal fungi;
Water status;
Phosphorus;
Vegetative growth.

INTRODUCTION

The favorable effects of mycorrhizal symbiosis on water and nutrients absorption by plants are not to demonstrate. Since its observation for the first time by Giuseppe Gibelli in 1879, many researchers have studied it on different plants and several studies have been published on this subject[1-4]. This symbiosis has attracted much interest for its use to mitigate stress effect on plants after obtaining synthetic strains since 1967 by Anna Fontana[5]. Since then and with development of molecular biology techniques and genetic analysis, several strains of mycorrhizal fungi were isolated, synthesized and tested on different plants. Especially for woody species, the emphasis was laid on symbiosis with

Regular Paper

arbuscular mycorrhizal fungi (AMF), belonging particularly to Glomus genus, for their encouraging results on implementation of these species in arid and semi-arid areas[6,7].

AMF are the most prevalent type of mycorrhizae and oldest who have co-evolved with terrestrial plants for at least 460 million years and are actually unable to survive without a host plant[8]. They are able to colonize and significantly improve growth of many plants, including woody species such as peach tree[9], peach-almond hybrids tree[10] and apple tree[11]. Hyphae of these mycorrhizae penetrate plant root cortex where they form intracellular arbuscles and vesicles. Arbuscles are the place of contact and exchange of elements between the two symbionts and vesicles constitute storage organs. Extra-root hyphae also grow over several centimeters outside from the root and may bear a multitude of spores that are the reproductive organs of mycorrhizae[12]. In symbiosis, the two partners mutually exchange elements necessary for their proper development: mycorrhizal fungi convey water and nutrients to the plant in exchange for carbon molecules coming from photosynthesis.

It is widely accepted that AMF plays an important role in host plant adaptation to drought[13,14]. However, the underground nature and the fact that a part of the fungal biomass is included inside roots make that some mechanisms of this symbiosis are unknown, although significant progress in the understanding of these mechanisms has been made with development of ecophysiology and biotechnology techniques. Possible mechanisms of AMF positive effects could be related to increase of root hydraulic conductivity[15], improvement of stomatal regulation and transpiration rate[16], forcing of water absorption even under low soil moisture by the extraradical mycorrhizal hyphae, osmotic adjustment which promotes maintenance of cell turgor, even at low water potential of tissues[17] and increase of photosynthetic activity by improving nutrients absorption[18]. Furthermore, Fitter[19] and Safir *et al*.[20] claimed that the influence of AMF on plant water relations may be a secondary consequence of an increase of minerals absorption, especially phosphorus. But the verification tests of this hypothesis have produced controversial results. Indeed, Nelson[3] found that water relations of onion were improved with increase of phosphorus concentration. Conversely, on rose and pepper plants, Augé *et al*.[17] found different levels of plant water stress resistance under the same phosphorus concentration.

Use of AMF may be a promising technique to improve water use efficiency of various plants subjected to water stress and save irrigation water. This technique would be particularly justified on plants that require higher quantity of irrigation water such as peach trees. It is in this in mind that was carried this work to quantify the effect of inoculation of young peach trees by arbuscular mycorrhizae, *Glomus intraradices* and *Glomus mossaea*, submitted to water stress under field conditions.

MATERIALS AND METHODS

Plant material and cultural conditions

The trial was carried out under field conditions in experimental station Ain Taoujdate of the National Agronomic Research Institute, located 40 km north of Meknes city (33° 56 'E, 5° 13' N, 499 m) northern Morocco. The soil is sandy clay containing an average of 7.7% $CaCO_3$, moderately rich in organic matter in surface (0-30 cm), with an average of 2% (0.92% in deep layer 30-60 cm). Soil pH is approximately neutral (7.3) and not saline with an electrical conductivity of 0.13 mS/cm in the first 60 centimeters.

The plant material used come from 48 young plants of four peach varieties, highly cultivated in Morocco: *Elegante*, *Equenene*, *Ziger* and *Fantazia*, grafted on *Pêcher de missour*, a local peach rootstock characterized by good compatibility, medium vigor, consistency production and longevity[21]. The plants were planted in January with spacing of 5x4m in the experimental field where the soil was previously homogenized by cover crop. Before planting, the terminal roots were partially cut to stimulate plant growth and promote mycorrhizal inoculation. Root inoculation was realized by 12 g/plant of an inoculum purchased on market containing 25 spores/g of *Glomus intraradices* and 25 spores/g of *Glomus mosseae*. The choice of these strains is based on

their high ability to colonize prunus rootstocks, demonstrated in previous research[22,10]. After planting, the plants were pruned, fertilized (N-P2O5-K2O = 60-40-80 kg/ha) and treated in the same way, except irrigation that was varied to produce two water regimes: 100% and 50% of crop evapotranspiration (ETc) during period of rainfall deficit, from January to October. ETc values were estimated as the product of reference evapotranspiration (ETo) obtained with the Hargreaves model[23] and the crop coefficients recommended by FAO adjusted to planting density and foliage dimensions using a reduction coefficient (Kr) recommended for almond tree: Kr = $\pi D^2 N/20000$ where "D" is the average of foliage diameters and "N" is planting density[24].

The experimental design was a criss cross with three variable factors: water regime (50% ETc and 100% ETc), mycorrhization (M + and M-) and peach variety. Indeed, the experimental orchard was divided into two equal and homogenous plots, one of which was fully irrigated (100% ETc) and another was submitted to water stress of 50% ETc. Each of the two plots contains 24 young peach plants with six randomized plants per variety of which three were inoculated by mycorrhizae and another three are not inoculated.

Measurements

Mycorrhizal and sporulation rates

Mycorrhizal rate was determined at the end of plant growth in November on root collected from soil samples (approximately 250 g/plant) taken from root zone. The collected roots were washed thoroughly with distilled water and preserved in a lactoglycerol solution (63 ml glycerol, 62 ml distilled water, 875 ml of acetic acid). Staining of root was realized on fragments measuring approximately 1 cm following the method of Hayman and Philips[25]. Indeed, the roots fragments were placed in 10% KOH solution in a bain-marie set to a temperature of 90 °C for 2 hours. Then they were washed with distilled water and transferred into 2% HCl solution for 5 min before being placed in a staining solution (lactoglycerol with 0.05% trypan blue) in bain-marie at 90 °C for 15 min. After staining, the Mycorrhizal rate was estimated under an optical microscope (x 100) from the number of fragments showing arbuscles or vesicles on the total colored fragments.

On soil samples collected from the root zone of mycorrhizal peach trees was counted number of the mycorrhizal spores. Indeed, an amount of 200 g of soil of each sample was softly stirred in 3 liters of distilled water and let to decant for 5 to 10 seconds, until the precipitation of the large particles of soil. The soil solution in suspension was passed through a series of piled sieves under tap water (250 µm, 106 µm and 63 µm). The fraction retained on the latest sieve (63 µm) was recovered and placed in a 50 ml conical tube whose the level is adjusted with distilled water to 25 ml. Using a syringe, 20 ml of a sucrose solution (50% w/w) was added in tube bottom. The tubes are then passed to the centrifuge (1000 rpm for 5 min). At the end of the centrifugation, the spores are concentrated to the sucrose-water interphase, that were collected using a pipette and sieved again (63 µm) to eliminate sugar residues. Finally, spores are isolated, placed in a petri dish containing 100 µl of distilled water and counted under a binocular microscope.

Vegetative growth measurements

The effect of water stress on vegetative growth of mycorrhizal and non-mycorrhizal peach trees was evaluated toward the end of their growth cycle, in October. The measurements concerned plant height, annual growth of trunk section, primary shoot length, secondary shoots length, number of secondary shoots per linear meter of primary shoot and leaf area.

The plant height was measured from collar graft to the highest apex. The annual growth of trunk section was estimated by measuring trunk circumference at the beginning and the end of plants growth cycle at 10 cm of soil. The average of primary and secondary shoot elongation was determined by measuring the final length of all shoots per plant. The leaf area was evaluated on twenty fully developed leaves per plant, taken from medial portions of the primary shoots.

Plants water status measurements

Plants water status was evaluated by monitoring predawn leaf water potential (Ψ_{pd}), midday leaf

Regular Paper

water potential (Ψ_{md}), midday stomatal conductance (gs) and midday leaf relative water content (RWC) in five different dates during plant growth cycle.

Ψ_{pd} was measured in the morning by a Scholander pressure chamber on two leaves per plant taken from shoot extremity (4th and 5th leaf), previously bagged by aluminum paper at sunset of the day preceding measurement. Ψ_{md} was measured on two leaves per plant taken from shaded shoot extremity.

On selected leaves for measuring Ψ_{md}, was measured stomatal conductance. At the same time (13h GMT), five fully developed leaves per plant were taken from shaded shoot extremity to measure the relative water content. This parameter was determined following the formula of Turner[26]:

$$RWC = \frac{FW - DW}{SW - DW} \times 100$$

Where FW, DW and SW respectively designate fresh, dry and saturation weights of leaf sample. Leaves were saturated by placing their petioles in contact with water in boxes papered inside with wet filter paper for 24 hours in a refrigerator set at 5 °C and they were dried in an oven at 105 °C for 48 hours.

Leaf phosphorus content

Leaf phosphorus content was determined on leaf samples taken from the middle portions of shoots toward the end of plant growth cycle, in October. Phosphorus analysis was performed according to the method described by Rayan et *al.*[27]. Indeed, phosphorus was extracted on samples dried using a mixture of ammonium molybdate, ammonium vanadate and nitric acid and quantified by spectrophotometer set at 410 nm.

RESULTS AND DISCUSSION

Rates of AMF colonization and sporulation

All the inoculated plants were successfully colonized by AMF with varied colonization rates depending on water regime (TABLE 1). The differences between varieties were not significant because of use of the same rootstock.

Even under full irrigation, colonization rate was relatively low with an average of 42% for the four tested varieties. The low AMF colonization rate stems from the fact that under field conditions, colonization of new ramifications of root system by AMF is confronted to various constraints including essentially the remoteness of many rootlets from AMF spores and the development of weeds that compete the young plants as to mycorrhizae[28]. Under water stress, the AMF colonization rate was significantly reduced by an average of 42% for the four tested varieties. The mechanisms of this inhibition due to water stress are associated with a low rate of spore germination and disturbance of chemical transmission between fungus and roots[29].

As for AMF sporulation rate, it varied little following genotypes, but it was greatly affected by water regime. In response to water stress, this rate increased amply by an average of 170% to pass from 54 spores/100g of soil observed under full irrigation to 146 spores/100g of soil under water stress. This rise of AMF sporulation rate indicates that level of the applied stress (50% ETc) was sufficient to induce the passage of mycorrhizal fungi to sporulation which constitutes their form of resistance to water stress[29].

Vegetative growth

Vegetative growth of all tested peach varieties, mycorrhizal and non-mycorrhizal, was affected by water stress of 50% ETc. However, the affected

TABLE 1 : AMF root colonization and sporulation rates under full irrigation (R100) and water stress of 50% ETc (R50)

	Water regime	Peach varieties				Average for specie
		Elegante	Equenene	Ziger	Fantazia	
AMF colonization rate (%)	R100	42.1 a	34.3 a	50.3 a	42.6 a	42.3 a
	R50	18.2 b	22.5 b	34.5 b	22.3 b	24.4 b
AMF spores density (spores/100g soil)	R100	56 a	58 a	53 a	51 a	54 a
	R50	143 b	156 b	132 b	152 b	146 b

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TABLE 2 : Vegetative growth parameters of mycorrhizal and non-mycorrhizal peach plants under different water treatments

			Trunk growth (mm/year)	Plant height (cm)	Primary shoot (cm)	Secondary shoot (cm)	Number of secondary shoot (N/Lm)	Leaf area (cm^2)
Elégante	R100	M+	13.8	2.1	103.3 c	23.6 b	9.4 b	50.6
		M-	12.7	1.9	93.3 bc	19.5 ab	9.6 b	48.9
	R50	M+	15.9	2.0	86.3 ab	19.0 ab	9.4 b	49.3
		M-	12.8	1.9	75.0 a	12.5 a	7.7 a	48.1
Equenene	R100	M+	15.9	2.2	99.4 b	34.1 b	11.2 a	51.4
		M-	10.6	2.1	100.1 b	26.6 ab	9.2 a	50.2
	R50	M+	20.2	2.1	93.3 ab	26.1 ab	8.6 a	50.1
		M-	15.9	2.0	84.0 a	12.6 a	7.1 a	49.3
Ziger	R100	M+	20.2	2.2	102.3 b	12.2 ab	9.8 d	52.2
		M-	13.8	2.0	96.7 ab	11.9 ab	9.0 c	49.7
	R50	M+	13.7	2.3	105.0 b	15.5 b	8.6 b	52.6
		M-	8.13	2.1	90.3 a	8.8 a	7.4 a	51.0
Fantazia	R100	M+	15.9 b	2.0	106.7 b	23.3 b	9.0 b	48.9
		M-	11.7 b	1.9	96.7 ab	22.7 b	9.4 b	48.5
	R50	M+	3.2 a	1.7	71.0 ab	14.7 ab	8.9 b	45.2
		M-	1.1 a	1.6	65.0 a	12.9 a	7.6 a	44.8
Average of specie	R100	M+	16.5	2.1	102.9 c	23.3 b	9.8 c	50.7
		M-	12.2	2.0	96.7 bc	20.1 ab	9.3 bc	49.3
	R50	M+	14.9	2.0	88.9 ab	18.6 ab	8.9 b	49.4
		M-	10.9	1.9	78.6 a	11.7 a	7.4 a	48.3

(N/Lm: number per linear meter)

parameters differed depending on varieties. For all varieties, water stress applied induced a significant decrease of shoots length and number of secondary shoots per linear meter of primary shoot, both in mycorrhizal and non-mycorrhizal plants TABLE 2. This depressive effect of water stress was also significant for trunk growth, but only in *Fantazia* variety. However, plant height and leaf area remained unchanged in all varieties tested. These depressive effects of water stress on plant growth were observed in similar works even under moderate water stress of 75% ETc[30,31].

Mitigation of water stress by AMF was partial, but statistically significant for all vegetative parameters affected. The mitigation rate due to AMF was 81% for primary shoot elongation, 92% for secondary shoot elongation and 96% for number of secondary shoots grown on linear meter of primary shoot. However, the decrease of trunk growth under water stress, observed only in *Fantazia* variety was not significantly alleviated by AMF although the obtained values show that there was a tendency to increase trunk diameter in mycorrhizal plants. Vegetative growth gain due to AMF was also observed for non-stressed plants, but with a relatively low magnitude. For all varieties, average of this gain was 6%, 16% and 5% respectively for primary shoot elongation, secondary shoot elongation and number of these latest per linear meter of primary shoot. This mitigation of water stress due to mycorrhizae comes mainly from their favorable effects on nutrient uptake and plant water relations under water stress conditions, as has been demonstrated on several plants in previous studies[32-34].

Peach plants were therefore significantly dependent to mycorrhizal fungi under the level of water stress tested. However, it should be noted that it is often assumed that dependency of plants to arbuscular mycorrhizae decreases with water stress to cancel at severe stress[35,32]. This decline of AMF effect under severe water stress is essentially explained by ineffectiveness of mycorrhizal fungi at

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TABLE 3 : Leaf phosphorus content (% DM) of mycorrhizal and non-mycorrhizal plants at the end of their growth cycle under different water regimes

		Elegante	Equenene	Ziger	Fantazia	Average of specie
R100	M+	0.38 b	0.39 b	0.34 c	0.42 c	0.38 c
	M-	0.39 b	0.37 b	0.34 c	0.41 c	0.38 c
R50	M+	0.30 ab	0.33 b	0.29 b	0.32 b	0.31 b
	M-	0.24 a	0.23 a	0.22 a	0.25 a	0.24 a
Signification		P=0.002	P=0.003	P=0.001	P=0.001	P=0.001

very low soil water potential, which would be attributed to low germination of spores and to mycorrhiza-soil-plant interactions[36]. Furthermore, mycorrhizal dependency of plants was relatively low under full irrigation, but statistically significant. The weakness of the mycorrhizal dependency under this latter water regime is explained by the low biomass gain observed in mycorrhizal plants, limited by the genetic growth potential of cultivars[37].

Leaf phosphorus content

The imposed water stress decreased phosphorus uptake for all non-mycorrhizal plant by different amounts following varieties, with an average of 37% TABLE 3. This result is in agreement with many works studied phosphate nutrition of plants under water stress[38,39]. Reduction of leaf phosphorus content in stressed plants is certainly not related to a deficiency of this nutrient in soil solution, but rather to a decrease of number of rootlets in response to water stress, which constitute the essential seat of mineral uptake[40].

This depressive effect of water stress on phosphorus uptake was significantly attenuated by AMF by 77% observed for *Elegante* variety to 100% for *Equenene*, with an average for specie of 81%. The significant improvement of leaf phosphorus content in mycorrhizal plants comes from extra-root hyphae of AMF that operate as additional rootlets and also to their ability to ramify the root system[41,42], thereby boosting nutrients uptake, including phosphorus. Mycorrhizal hyphae does not only explore the available phosphorus contained in soil solution, but they also have the ability to access to non-assimilable phosphorus and that integrated in organic matter by secreting phosphatase enzymes and various molecules that acidify the soil, making phosphorus more available[43].

However, AMF has not had a significant effect on phosphorus uptake under full irrigation, although the obtained values generally show a tendency to a slight improvement of phosphorus uptake under this water regime. The non-significance of AMF effect under this water regime may be explained by the fact that the amount of rootlets developed by non-mycorrhizal plants under full irrigation was sufficient to uptake phosphorus at the similar level than mycorrhizal plants.

Plant water status

Plant water status was very influenced by water stress. Significant reductions of midday leaf water potential (Ψ_{md}), relative water content (RWC) and stomatal conductance (gs), measured at midday, were observed immediately on non-mycorrhizal plants upon application of water stress (Figures 1, 2, 3), such as has been found in previous works on rosaceous fruit trees including peach[44-46]. Over the monitored period, from May 07 to July 04, Ψ_{md} values were decreased by an average of -0.30 MPa for all tested varieties. RWC and gs values ecreased by similar manner of Ψ_{md} values. Highly significant correlation was found between these parameters indicating this similarity (Figure 4). Values of gs decreased by an average of 27%. However, RWC decrease was relatively low with an average of 5%, compared to control treatment (non-mycorrhized).

Water stress applied did not induce immediate changes for predawn leaf water potential (Ψ_{pd}) values, whose values have remained unchanged for a period of three months after stress application, from March to May. However, with increase of crop evapotranspiration since June, Ψ_{pd} values began to decrease significantly in response to water stress, with an average of -0.15 MPa over the period from June 05 to July 04 (Figure 5). According to Lampinen

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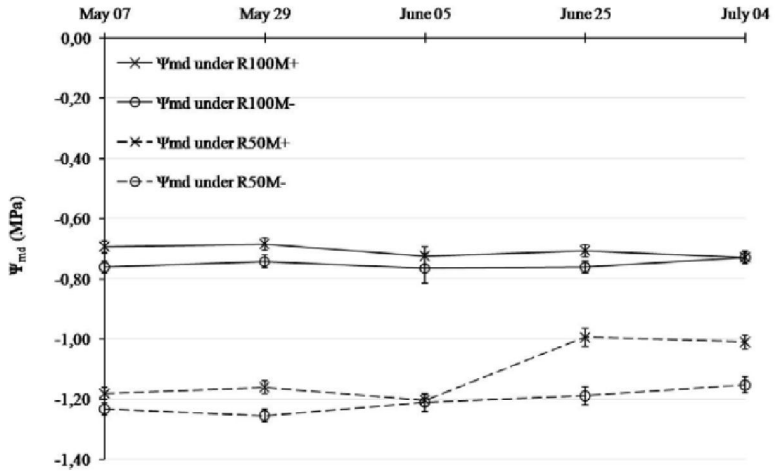

Figure 1 : Seasonal variation of midday leaf water potential (Ψ_{md}) of mycorrhizal (M+) and non-mycorrhizal (M-) young peach tree under full irrigation (R100) and water stress of 50% ETc (R50) (average values for all tested varieties)

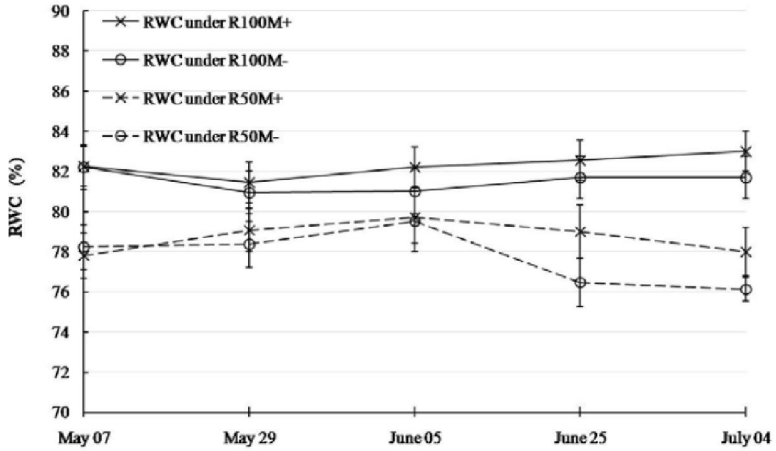

Figure 2 : Seasonal variation of midday leaf relative water content (RWC) of mycorrhizal (M+) and non-mycorrhizal (M-) young peach tree under full irrigation (R100) and water stress of 50% ETc (R50) (average values for all tested varieties)

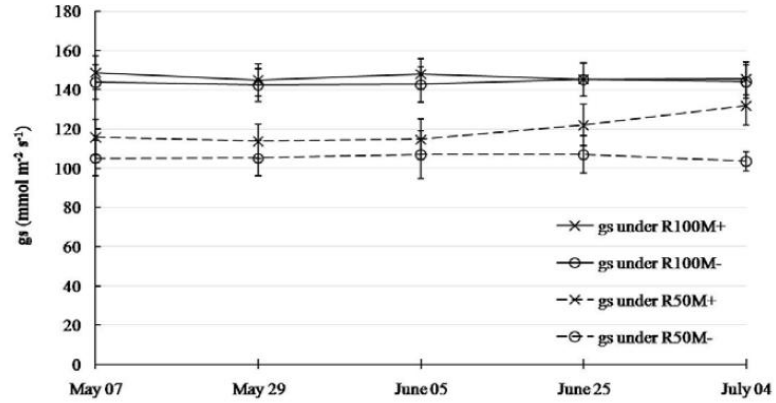

Figure 3 : Seasonal variation of midday stomatal conductance (gs), of mycorrhizal (M+) and non-mycorrhizal (M-) young peach tree under full irrigation (R100) and water stress of 50% ETc (R50) (average values for all tested varieties)

et al.[45], Ψ_{pd} decrease is explained by the fact that root system of young trees is not sufficiently developed to explore all the moist parts of root zone and thereby stabilize Ψ_{pd} values .

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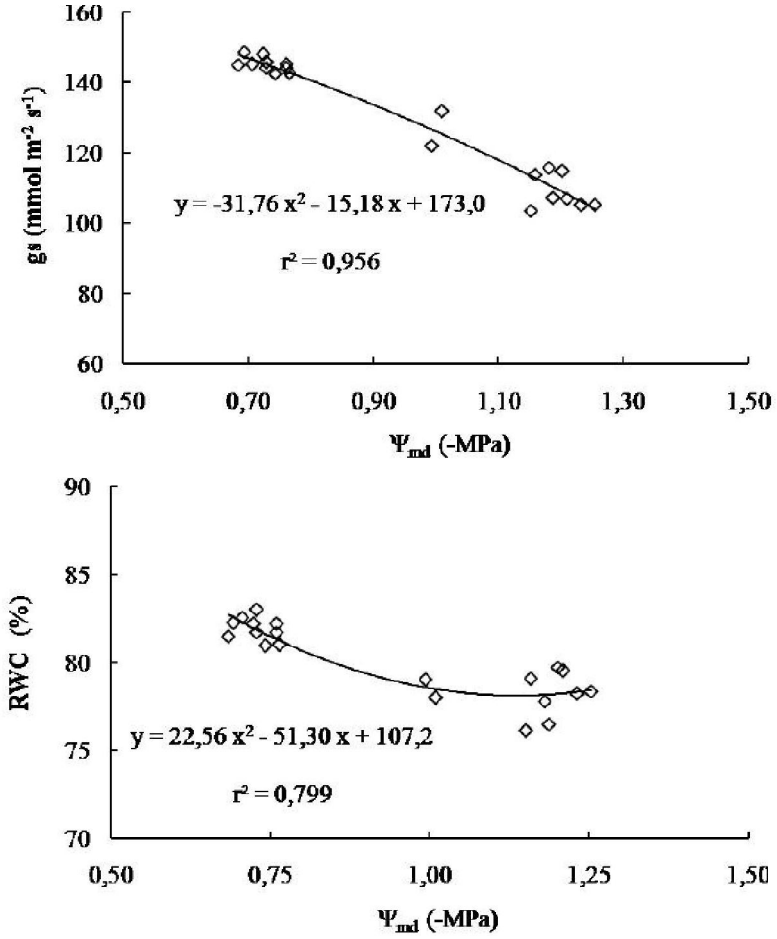

Figure 4 : Relationship between relative water content (RWC), stomatal conductance (gs) and water potential (Ψ_{md}) measured at midday (all varieties and treatments combined)

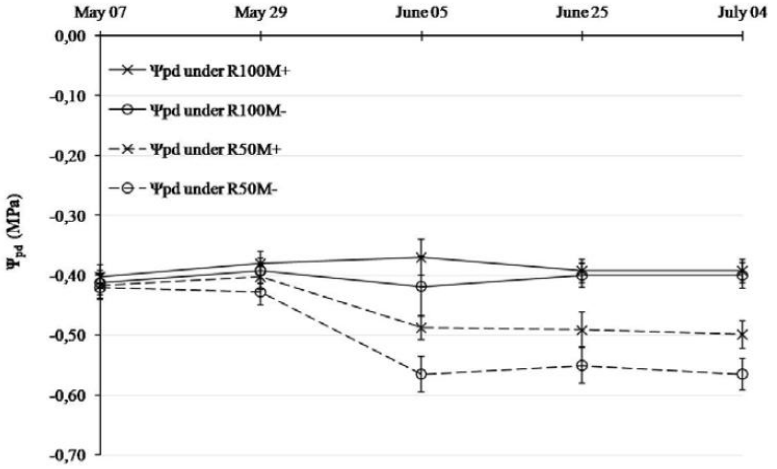

Figure 5 : Seasonal variation of predawn leaf water potential (Ψ_{pd}) of mycorrhizal (M+) and non-mycorrhizal (M-) young peach tree under full irrigation (R100) and water stress of 50% ETc (R50) (average values for all tested varieties)

However, water stress effect on plant water status was partially mitigated by AMF. Mitigation effect due to AMF was significant for Ψ_{md} and gs values. However, RWC values were not significantly affected by AMF although this parameter was significantly correlated with Ψ_{md}. According to works of Liu *et al.*[47], Duan *et al.*[48] and Davies *et al.*[49], this result indicates that under conditions of the

present experiment, AMF induced an increase of Ψ_{md}, Ψ_{pd} and gs values in colonized plants by improvement of stomatal regulation and adjustment of osmotic potential through biochemical signals including essentially ABA and modification of hormonal balances, but without boosting water absorption, although this latter effect is known as a benefit of mycorrhizae[50]. A further explanation for this result is that AMF ensure maintenance of leaf cells turgor through accumulation of solutes, thereby stabilizing water potential and stomatal conductance values without changing leaf water content[51,48].

These changes induced by water stress and AMF on plant water status were not statistically different between varieties. Indeed, variance analysis of Ψ_{pd}, Ψ_{md}, gs and RWC values at July 04, when the effects of water stress and AMF were more marked, revealed no significance differences between the tested varieties under all treatments (TABLE 4). This observation is explained by the fact that the tested varieties were grafted on the same rootstock and / or by similarity of hydro-mineral requirements between the tested varieties.

TABLE 4 : Significance of means variance analysis of water status parameters observed at July 04 depending on peach varieties

		Ψ_{pd}	Ψ_{md}	RWC	gs
R100	M+	P = 0.968	P = 0.846	P = 0.56	P = 0.662
	M-	P = 0.984	P = 0.863	P = 0.782	P = 0.851
R50	M+	P = 0.754	P = 0.856	P = 0.759	P = 0.854
	M-	P = 0.975	P = 0.880	P = 0.874	P = 0.697

CONCLUSION

In this experiment, we evaluated the capacity of arbuscular mycorrhizal fungi (*Glomus intraradices* and *Glomus mosseae*) to alleviate water stress effects on young peach tree under field conditions. We found that without mycorrhizal fungi, the young peach tree does not tolerate water stress of 50% ETc. Plants response to water stress was marked by a significant deterioration of their nutritional and water status, thereby inducing considerable reductions of their vegetative growth. The arbuscular mycorrhizal fungi have partially offset effects induced by water stress. The favorable effect of mycorrhizal fungi was not due to an improvement of plants relative water content, but rather to a partial stabilization of water potential and stomatal conductance. Arbuscular mycorrhization was therefore able to improve water and nutrient use efficiency of the young peach trees, but it was unable to make them tolerant to water stress of 50% ETc. However, for optimal deficit irrigation of young peach in semi-arid areas, the obtained results suggest adoption of water regime of 50% ETc associated to mycorrhizal symbiosis in extent that this water regime did not induces a consistent reductions of plants growth, compared to full irrigation.

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