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ORIGINAL PAPER

Mycorrhizal association between the desert truffle *Terfezia boudieri* and *Helianthemum sessiliflorum* alters plant physiology and fitness to arid conditions

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Abstract The host plant *Helianthemum sessiliflorum* was inoculated with the mycorrhizal desert truffle *Terfezia boudieri* Chatin, and the subsequent effects of the ectomycorrhizal relationship on host physiology were determined. Diurnal measurements revealed that mycorrhizal (M) plants had higher rates of photosynthesis (35%), transpiration (18%), and night respiration (49%) than non-mycorrhizal (NM) plants. Consequently, M plants exhibited higher biomass accumulation, higher shoot-to-root ratios, and improved water use efficiency compared to NM plants. Total chlorophyll content was higher in M plants, and the ratio between chlorophyll *a* to chlorophyll *b* was altered in M plants. The increase in chlorophyll *b* content was significantly higher than the increase in chlorophyll *a* content (2.58- and 1.52-fold, respectively) compared to control. Calculation of the photosynthetic activation energy indicated lower energy requirements for CO_2 assimilation in M plants than in NM plants (48.62 and 61.56 kJ mol^{-1}, respectively). Continuous measurements of CO_2 exchange and transpiration in M plants versus NM plants provided a complete picture of the daily physiological differences brought on by the ectomycorrhizal relationships. The enhanced competence of M plants to withstand the harsh environmental conditions of the desert is discussed in view of the mycorrhizal-derived alterations in host physiology.

Keywords Photosynthesis · Transpiration · Activation energy · Chlorophyll b · Gas exchange

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Introduction

Mycorrhizal symbiosis improves nutrient and water absorption from the soil via the external fungal hyphae. In return, the fungus acquires photoassimilates from the host. This type of mutualistic relationship exists in the majority of plant ecosystems and accounts for plant growth and nutrient cycling (Smith and Read 2008). Through the exploration of comparatively larger soil volumes and the faster movement of minerals into the hyphae, mycorrhizal (M) plants exhibit higher growth and development rates than non-mycorrhizal (NM) plants (Estrada-Luna et al. 2000; Fan et al. 2008; Manoharan et al. 2010; Martins et al. 1997; Reid et al. 1983). Under arid conditions, characterized by limited water supply and mineral availability (mainly P and N), the contribution made by mycorrhizal fungi to plant development and survival are of greater importance (Morte et al. 2000; Navarro-Ródenas et al. 2010).

Terfezia boudieri (Pezizaceae) is a desert truffle that forms a mycorrhizal association with its host plant *Helianthemum sessiliflorum* (Cistaceae), a small, perennial desert shrub, and with other species of this family (Kagan-Zur et al. 2008; Percudani et al. 1999; Trappe 1979). *Helianthemum* spp. and *Terfezia* spp. are distributed throughout the Mediterranean Basin, northern Africa, Saudi Arabia, and the United Arab

Emirates, where truffles play important roles in both folklore and cuisine (Mandeel and Al-Laith 2007). *Terfezia* spp. are capable to form under certain conditions several types of mycorrhizal associations, including endo, ectendo, and ectomycorrhiza (Dexheimer et al. 1985; Fortas and Chevalier 1992; Zaretsky et al. 2006). Similar to other mycorrhizal associations, *Helianthemum* spp. inoculated with *Terfezia* spp. exhibit increased plant development due to higher net photosynthesis (Pn) rates (Fan et al. 2008; Morte et al. 2000; Reid et al. 1983). The augmented photosynthetic activity can be partially explained by improvements in nutrient uptake, stomatal conductance, increased total chlorophyll content, and the adjustment of photosynthetic activity to the strong carbon demand of infected roots (Dosskey et al. 1990; Kaschuk et al. 2009; Morte et al. 2000; Nehls 2008). To date, comparisons of the CO_2 exchange rates of M plants and of NM plants were limited by technical constraints, such as partial daytime measurements that were usually preformed at maximal light intensity. Thus, comprehensive diurnal comparisons of CO_2 exchange and water status between M and NM plants during a 24-h period are lacking and the currently available published data are incomplete. It is therefore imperative to our understanding of how mycorrhizal associations contribute to their host plants' development and survival in arid zones, to describe diurnal CO_2 exchange and transpiration (E) rates with and without symbioses. We set the experimental conditions to meet the natural conditions prevailing in spring time when carbon and water demands by both partners peaks. Growth-resuming, flowering of the host and the fungus fruiting season impose large carbon sinks that requires higher efficiency of the photosynthetic apparatus. In this study, we used an automatic photosynthesis and transpiration monitor (PTM) that enables continuous measurements. The aim of this work was to examine the physiological performance of *H. sessiliflorum* during mycorrhizal association with the desert truffle *Terfezia boudieri* and to provide a complete picture of the host's daily physiological performance.

Materials and methods

Plant and fungal material

Seeds of *H. sessiliflorum* were collected in the wild. The seeds were surface sterilized in sodium hypochlorite solution diluted to 1% of commercial bleach for 5 min and rinsed three times with sterile doubly distilled water. Seeds were germinated under sterile conditions at pH 6.0 on M medium (Bécard and Fortin 1988) that was solidified with 0.9% Bacto agar (Acumedia Manufacturers, Inc., Baltimore, MD, USA). Three months after germination the seedlings were transferred to sterile, sand-containing pots, at which time they were inoculated with *T. boudieri* culture that was grown from fresh fruiting bodies on Fontana medium (Bonfante 1973) amended with 25 μg/ml streptomycin (Roth-Bejerano et al. 1990). The inoculated seedlings were grown for one month and then transferred to 20-L pots containing 30 kg of autoclaved sandy soil collected from the natural habitat of *H. sessiliflorum* in the Negev desert, Israel. Control plants were prepared similarly except for the inoculation procedure. The plants were irrigated using a 2-L h^{-1} dripper three times a week for 2 h. Fungal colonization in the roots was assessed as previously described (Kagan-Zur et al. 1994). We verified that root of control plants were not inoculated by staining and observation under light microscope.

Experimental conditions

The study was conducted in Beer-Sheva, Israel, in a greenhouse equipped with ventilating cooling systems that maintained a minimum humidity of 23% at noon and a maximum humidity of 80% at night. The midday temperature ranged between 30°C and 36°C and the nighttime temperature was around 20°C. The plants were grown in the greenhouse from May 2009 until their harvest in December 2009.

Chlorophyll and carotenoid content

Leaf chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), and total carotenoids were extracted with 80% aqueous acetone and the absorbance values of the extract at 470, 663.2, and 646.8 nm were determined with a spectrophotometer (UVmini-1240, Shimadzu, Japan). Chlorophyll and carotenoid concentrations were calculated using the equations previously described (Lichtenthaler 1987).

Photosynthesis, transpiration, temperature, and radiation

Physiological measurements were carried on 8-month-old plants grown in a greenhouse as described above. Photosynthesis and transpiration measurements were taken with a PTM-48A (Photosynthesis and Transpiration Monitor Bio Instruments 2007 SRL, Chisinau, Moldova), a new, portable device equipped with a four-channel automated system for monitoring CO_2 exchange and leaf transpiration (http://phyto-sensor.com/PTM-48A.en). Each of its four leaf cuvettes (self-clamping devices operated one at a time such that only one of the four leaf cuvettes is closed at any given time) has an area of 20 cm^2 and a radius of 2.5 cm. For most of the duration of the experiment, therefore, the sample leaves were not disturbed, and the time needed to take a sample was negligible. CO_2 exchange was determined by measuring the decrement of CO_2 concentration at

the leaf chamber outlet, compared with its concentration in the incoming ambient air. Two of the four cuvettes were placed on M plants while the other two were on NM plants. Transpiration rate was similarly determined using the absolute concentration of water vapor in the air, such that absolute humidity was computed during a transient period between 20 and 30 s after closing the cuvette. The calculation algorithm takes into account the rising humidity inside the chamber, and hence, allows the initial transpiration rate to be determined at the ambient air humidity.

In addition to the photosynthesis sensor, the data logger of the monitor has inputs for other supporting sensors, and the current experiment also included taking measurements with radiation, air temperature, and humidity sensors. The combined measurements of canopy temperature and relative humidity (RH) enabled the monitor's software to determine the leaf-to-air vapor pressure deficit (VPD). Photosynthesis data, collected from fully developed leaves on four different plants in the greenhouse, and data from the additional sensors, were automatically recorded sequentially (logged for 30 s every 30 min), and the output was averaged. Thus, their long open times and short closing times maintained the environment inside the leaf cuvettes at approximately the same conditions as their surrounding environment.

We used the CO_2 exchange rate to describe diurnal CO_2 assimilation and emission and Pn to describe only photosynthesis, i.e., light time. The data were collected during three consecutive days from each plant (eight plants per treatment).

Plant growth

After 8 months of growth in the greenhouse, ten plants from each treatment were harvested and the shoot and root fresh weights (FWs) were determined. Shoot and root dry weights were determined after drying for 48 h at 75°C in an oven.

Photosynthetic activation energy

Photosynthetic activation energy of M and NM plants was calculated as described earlier (Ben-Asher et al. 2006). Briefly, a scatter diagram of all Pn values (positive CO_2 uptake rates) was plotted against the canopy temperature (Fig. 1). The graph's upper trend line, which indicates the maximum Pn rates at a particular temperature, was fitted to the measured points. The exponential portion of the curve was then used to calculate the minimum photosynthetic activation energy using the Arrhenius plot [Ln(Pn) vs. $1/T$], where T is the absolute temperature.

This approach may be valuable for modeling data with an exceptionally large range due to the impact of unaccounted variables, such as plant age, variation in RH due to irrigation, and plant location within the container. This methodology was used as described previously (Ben-Asher et al. 2008). It creates a curve that demarcates the upper limits of the scatter plot data and includes all the data points collected inside the envelope.

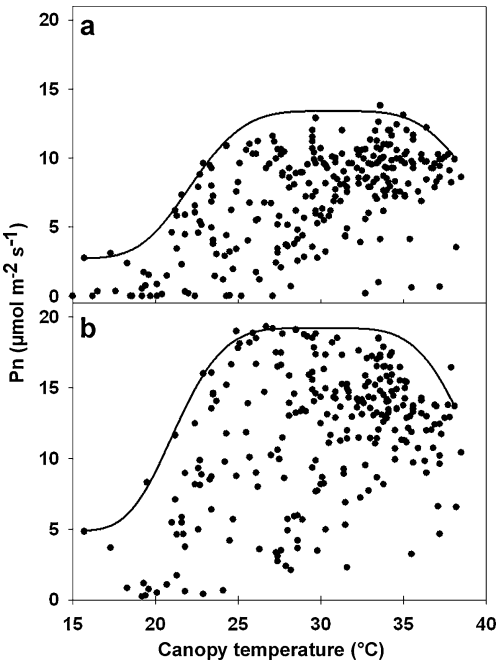

Fig. 1 Temperature dependence of the Pn rate for NM (**a**) and M (**b**) plants. Data were obtained at 30-min intervals at various temperatures for NM and M plants (282 and 266 data points, respectively). The envelopes for the rising portions were analyzed using the Arrhenius equation for calculating the activation energy presented in Table 3

Water use efficiency

Water use efficiency (WUE) was calculated by dividing the Pn value by the corresponding E value recorded at the same time point. Twelve hours of Pn data and E data (obtained at 30-min intervals) from 12 days were used to compare the WUE of eight M and NM plants each.

Statistical analysis

Each experiment was repeated at least three times, and the data were analyzed with JMP software. Treatment means were compared by the least significant difference using one-way ANOVA ($P<0.05$).

Results

H. sessiliflorum M plants exhibited higher rates of Pn than NM plants (Fig. 2a). The differences in Pn activity between

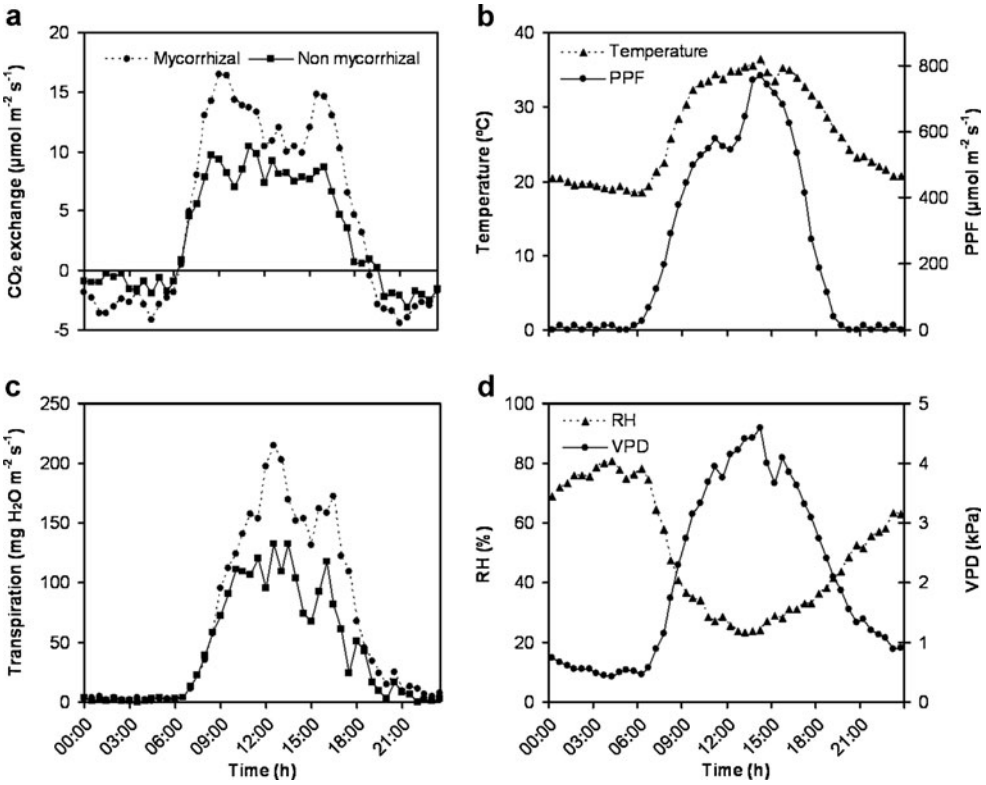

Fig. 2 M and NM *H. sessiliflorum* plants daily CO_2 exchange (**a**). Photosynthetic photon flux (*PPF*) and ambient temperature (**b**). Transpiration rates of M and NM *H. sessiliflorum* plants (**c**). Relative humidity (*RH*), and vapor pressure deficiency (*VPD*) (**d**). Eight plants were analyzed in each treatment. The data presented are the means for each treatment of two plants analyzed on the same days

the treatments were both quantitative and qualitative, as reflected in the different patterns of photosynthetic activity. Already in the early morning (7:30 a.m.), 2 h after sunrise, Pn rates for M and NM plants were distinctly different (Fig. 2a) and were maintained as such throughout the day. Moreover, M plants exhibited two distinct peaks at 10:00 a.m. and 5:00 p.m. (Fig. 2a).

The 10:00 a.m. peak of photosynthetic activity in M plants was followed by a typical reduction in Pn between 12:00 p.m. and 2:30 p.m. (Fig. 2a). Later in the afternoon, however, photosynthetic activity of the M plants recovered to a level similar to that measured in the morning (Fig. 2a). In NM plants, in contrast, no distinct pattern of peaking photosynthesis and subsequent recovery was observed, possibly due to their less effective water uptake than M plants, despite being well-irrigated (Fig. 2a, c). Another notable difference observed in M plants was the timing of stomatal closure, which occurred 1 h later than in NM plants (Fig. 2a, c). Indeed, a comparison of the daily Pn values between M and NM plants revealed an average difference of 35.2% between the treatments, which is the outcome of the higher efficiency in the photosynthetic activity of M plants (Table 1). These experiments were carried in a greenhouse under moderate photosynthetic photon flux (PPF) levels (800 µmol m^{-2} s^{-1}, Fig. 2b). However, we repeated this experiment under open field conditions of high irradiance levels (2,000 µmol m^{-2} s^{-1}) with similar results (data not shown).

M plants had elevated night respiration rates that were 49.5% higher than in NM plants, indicating that M plants had increased metabolic activity (Fig. 2a).

The highest photosynthetic activity occurred in the morning and the afternoon when temperatures and VPD were comparatively low and relative humidity was high (RH was 75% in the morning compared to 25% at midday). During the morning, the E rates of NM and M plants were similar, whereas between noon and evening (12:00 p.m. to 6:00 p.m.), M plants exhibited higher E rates (Fig. 2c). The daily average difference in E rates between the treatments was 18.3% (Table 1).

The higher photosynthetic activity of M plants was reflected in the total plant biomass gained during the experiment (Table 2). Accordingly, M plants gained significantly more biomass, based on both fresh and dry weights, than did NM plants. Plant inoculation resulted in enhanced shoot development by 3.5-fold (FW-based) compared to NM plants (Table 2). However, compared to NM plants, the fresh weight of roots from inoculated plants was only 1.7-fold higher. The shoot to root ratio, (based on dry weights) was about twofold higher. Hence, inoculation with the fungus enabled larger canopy development (1.9-fold) relative to root development (1.31-fold), an outcome of the mycorrhizal support in the M plants.

Plotting Pn values against E values revealed the contribution to the physiological performance of the host plant made by the mycorrhizal association (Fig. 3a). The

Table 1 Mean photosynthesis (Pn), night respiration, and transpiration (E) rates of M and NM plants

Treatment	Pn (mol $m^{-2}12\ h^{-1}$)	Night respiration (mol $m^{-2}12\ h^{-1}$)	E (mol $m^{-2}12\ h^{-1}$)
M	0.56±0.01a*	0.13±0.01a*	229.80±11.23a*
NM	0.36±0.01b*	0.07±0.01b*	184.46±15.55b*
Mean difference	35.2±1.7%	49.5±3.0%	18.3±4.4%

Measurements were made during May and June 2009. Means in each column followed by different lowercase letters are significantly different
*$P<0.05$

photosynthetic activity in M plants was significantly higher than in NM plants in the early morning, when E values were low, and it was similar between treatments (~50–100 mg H_2O m^{-2} s^{-1}). The Pn activity in M plants recovered to its high morning values in the late afternoon, when E rates, although lower than those at noon, were relatively high (~150–200 mg H_2O m^{-2} s^{-1}). The higher E rates of M plants indicate elevated stomatal conductivity, which facilitates CO_2 uptake (Fig. 2a, c). Although E rates in M plants were relatively higher than in NM plants, M plant WUE values were more than twofold higher than in NM plants (Fig. 3b). Moreover, the highest Pn activity occurred under low PPF levels (Fig. 2b), when photon flux should be a limiting factor for efficient photosynthesis. The higher Pn activity under low PPF can be attributed to the increase in total M plant chlorophyll content (Fig. 4). Analysis of the chlorophyll compositions revealed, as expected, that both Chl *a* and Chl *b* concentrations were significantly higher in M than in NM plants (Fig. 4). Chl *b* concentrations in M plants increased more than did Chl concentrations (2.4- and 1.52-fold, respectively). No significant differences were found in carotenoid concentrations between treatments (Fig. 4).

The increase in Chl *b*, the higher Pn rates under low PPF, and the significantly higher Pn rates under suboptimal temperatures (Fig. 1) collectively imply that the Pn activation energy in M plants is probably lower than in NM plants. Plotting Pn rates against canopy temperatures revealed that Pn rates increased exponentially (under both treatments) as the temperature arose above 15°C, but they reached a maximum at ~27°C (Fig. 1). At temperatures higher than 35°C, Pn rates declined in both treatments. In M plants, the increase between Pn rates measured at a suboptimal temperature (15°C) and those measured at an optimal temperature (27°C, maximal activity) was higher than in NM plants, in M plants Pn topped out at 19.2 μmol m^{-2} s^{-1}. In NM plants, whose rate of increase was slower, the maximum Pn measured was 11.6 μmol m^{-2} s^{-1} (Table 3). Calculating Pn activation energy revealed that the energy requirement for the assimilation of CO_2 in NM plants is 21% higher than in M plants.

Discussion

T. boudieri inoculation of *H. sessiliflorum* plants conferred significant developmental and physiological benefits on M plants when compared to NM plants (Fig. 2a, b and Table 1). The data presented here are in agreement with previous reports that showed a positive correlation between the presence of mycorrhizae on the root system with enhanced growth rates and Pn competence (Allen et al. 1981; Estrada-Luna et al. 2000; Fan et al. 2008; Morte et al. 2000). The differences in Pn rates between M and NM plants were most apparent during the morning and late afternoon, times of day characterized by low PPF intensity and relatively high humidity (Fig. 2c, d). Various mechanisms, which are the direct results of the *Terfezia*-driven physiological adaptations of the M plant that have endowed it with the ability to grow in arid zones, enable improved CO_2 uptake at low PPF levels. The increase in total chlorophyll content in the leaves of M plants facilitates

Table 2 Mean FW and DW measurements of shoots and roots of M and NM plants

Treatment	Shoot FW (g)	Root FW (g)	Shoot DW (g)	Root DW (g)	Shoot/root ratio
M	27.91±5.11a*	2.60±0.20a*	7.98±2.51a*	1.33±0.11a*	9.25±1.19a*
NM	7.98±0.98b*	1.78±0.19b*	4.60±0.58b*	1.01±0.12b*	4.65±0.26b*

Shoot to root ratio was calculated on a dry weight basis. Means in each column followed by different lowercase letters are significantly different
DW dry weight
*$P<0.05$

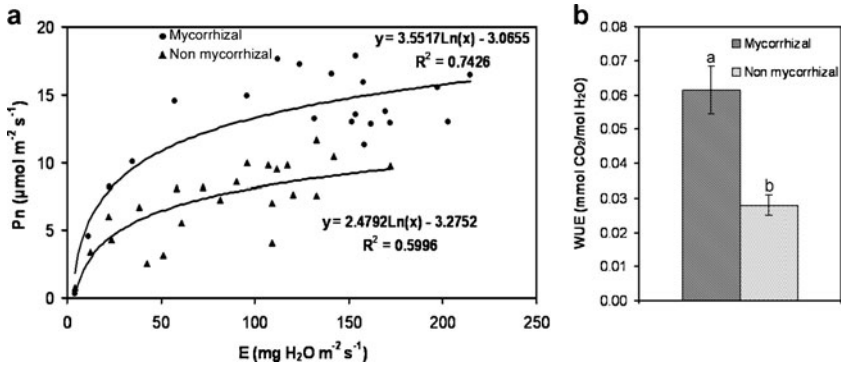

Fig. 3 Photosynthesis rate (*Pn*) plotted against transpiration rate (*E*) of M and NM plants (**a**). Plot data from a single day of analysis. WUE of M and NM plants (**b**). Eight plants were analyzed in each treatment. Different lowercase letters denote significant differences ($P<0.05$)

light harvesting activities. Furthermore, the specific increase in Chl *b* content improves light absorbance at lower energy wavelengths, and as such, it supports light harvesting under the lower irradiance conditions typical of mornings and afternoons (Chow et al. 1990; Melis and Harvey 1981). Under desert conditions water is scarce, and it becomes the most limiting factor for Pn activity and plant growth. The increase in Chl *b* allows improved Pn activity during those parts of the day when the ambient conditions are less extreme and water loss through open stomata is much lower. Although it was shown that many mycorrhizal plants have higher carotenoid contents (Krishna et al. 2005; Vodnik and Gogala 1994), this was not the case in our system, probably because the plants were grown under relatively moderate irradiation intensities (Fig. 4).

In the morning, there were no observed differences between the E rates of M and NM plants, but the differences between their Pn rates were at a maximum (Fig. 2a, c). By noontime, the Pn activity of M plants was significantly reduced in contrast to the plants' markedly increased E rates. This weak linkage between photosynthesis and transpiration is an inherent part of the plant strategy for maximizing WUE, a trait that is of paramount importance in habitats where water supply is limited (Fig. 3a). The response to high humidity was followed by a reduction in the leaf-to-air VPD, the driving force for transpiration, while stomata remained open to maintain effective photosynthesis. It seems, therefore, that the better WUE of M plants is mainly the outcome of the higher photosynthetic activity in the mornings at times when M and NM plants exhibit similar transpiration rates (Fig. 3a, b). It is interesting to note that although both treatments were grown under well-watered conditions, in mycorrhizal plants water uptake was higher than in control plants as reflected by higher rates of transpiration (Fig. 2c and Fig. 3b). This result indicates that improvement of the water status by mycorrhizal relations is not confined to water stress conditions.

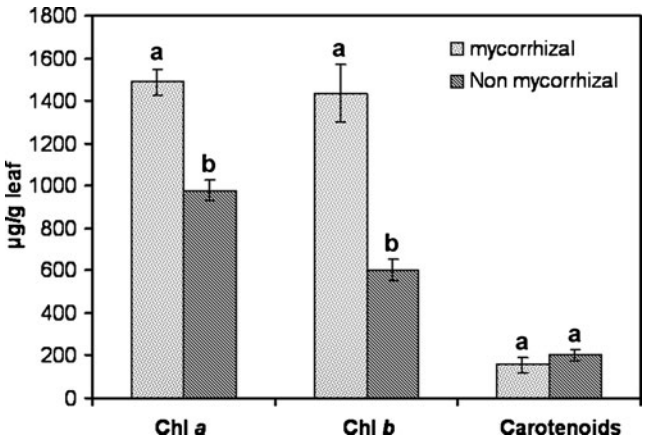

Fig. 4 Chl *a*, Chl *b*, and carotenoid contents of M and NM plant leaves sampled from plants 8 months post-germination; values are means±SE ($n=10$). Different lowercase letters denote significant differences ($P<0.05$)

H. sessiliflorum inoculation with *Terfezia* resulted in a significant decrease in the Chl *a*/*b* ratio from 1.6 in NM plants to 1 in M plants. A similar decrease in the Chl *a*/*b* ratio was observed when non-acclimated desert plants were exposed to high temperatures and drought stress (Armond et al. 1978; Loggini et al. 1999). This indicates that *Terfezia–Helianthemum* symbiosis may activate similar mechanisms whose function is to adjust photosynthetic activity to obtain relief from stresses such as heat or drought (Fig. 4). How the fungus exerts these alterations in the chlorophyll ratio, which gives M plants in a desert climate an ecological advantage, is currently unknown.

During the night, M plants had higher respiration rates than NM plants (Fig. 2a; Table 1). Collectively, the increases in Pn rates and night respiration indicate augmented metabolic activities that are reflected in the higher growth rates of the M plants (Table 2). Previous

Table 3 Photosynthetic activation energies and photosynthesis rates of M and NM plants at suboptimal (15°C) and optimal (27°C) temperatures

Treatment	Activation energy (kJ mol^{-1})	Pn at 15°C (µmol m^{-2} s^{-1})	Pn at 27°C (µmol m^{-2} s^{-1})
M	48.62	4.82	19.17
NM	61.56	2.74	11.58

reports on the carbon cost of maintaining the mycorrhizal association indicate the daily consumption of between 2% and 17% of the fixed photoassimilates by the fungus (Bryla and Eissenstat 2005). Although the actual cost of maintaining mycorrhizal symbiosis is varied, it is clear that a well-established mycorrhizal host plant is a stronger sink for the assimilated carbon (Table 2). The mycorrhizal association substantiates the potential of the host plant to develop and survive in harsh climates (Amaranthus and Perry 1989; Azcón-Aguilar and Barea 1997; Davies and Call 1990; Morte et al. 2000; Onguene and Kuyper 2002) in spite of the fungal carbon requirements to support hyphal growth and fruit body formation.

Photosynthetic efficiency is determined by, among other variables, leaf area, stomatal density, stomatal conductance, and the CO_2 gradient. M and NM *H. sessiliflorum* plants, however, had similar leaf sizes and stomatal densities (data not shown), findings that are in line with several previous works on both ecto- and endomycorrhizae, although in some cases increases in leaf area were noted (Estrada-Luna et al. 2000; Krishna et al. 2005; Manoharan et al. 2010). Therefore, we conclude that the improved Pn efficiency of M plants is the outcome of faster CO_2 removal and higher assimilation rates by the photosynthetic machinery. The calculated, lower photosynthetic activation energy (Table 3), and the findings of previous works demonstrating decreases in the intercellular CO_2 concentrations of M plants (Sheng et al. 2008; Zhu et al. 2010) add further support to the above conclusion. The lower M plant photosynthetic activation energy is indicative of the ability of the photosynthetic apparatus to operate efficiently under sub-optimal temperatures (Table 3). In other words, the reduction in photosynthesis activation energy allows M plants to maintain their photosynthetic capacities under unfavorable conditions and ultimately to produce larger amounts of biomass than NM plants. The latter result is consistent with an earlier work showing the beneficial contribution of the mycorrhizal association to Pn rates in plants grown under low-temperature stress (Xian-can et al. 2010). The increases in transpiration rates and chlorophyll content contribute to the reduction in photosynthesis activation energy, but additional factors possibly influenced by the mycorrhizal relationships, such as intensified photophosphorylation and the enhanced activity of the enzymes operating in the Calvin cycle, cannot be excluded.

The data presented here raise several fundamental questions about the mechanisms and the signals that affect host plant physiological performance. The molecular basis of fungal communication with its host, for example, is currently unknown. One possible candidate for such signal molecules may be the recently discovered family of small secreted protein effectors (Kagan-Zur et al. 2008; Martin et al. 2008).

In conclusion, the enhanced competence of mycorrhizal plants to persevere in the harsh environmental conditions of deserts is attributed to their higher CO_2 assimilation rates and higher WUE, which, in turn, are the outcomes of special adaptations, including increased Chl *b* content, lower photosynthetic activation energy, and enhanced stomatal conductance, that alter and improve the physiological performances of the host plant.

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