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ORIGINAL PAPER

Influence of arbuscular mycorrhizae on photosynthesis and water status of maize plants under salt stress

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Abstract The influence of arbuscular mycorrhizal (AM) fungus *Glomus mosseae* on characteristics of the growth, water status, chlorophyll concentration, gas exchange, and chlorophyll fluorescence of maize plants under salt stress was studied in the greenhouse. Maize plants were grown in sand and soil mixture with five NaCl levels (0, 0.5, 1.0, 1.5, and 2.0 g/kg dry substrate) for 55 days, following 15 days of non-saline pretreatment. Under salt stress, mycorrhizal maize plants had higher dry weight of shoot and root, higher relative chlorophyll content, better water status (decreased water saturation deficit, increased water use efficiency, and relative water content), higher gas exchange capacity (increased photosynthetic rate, stomatal conductance and transpiration rate, and decreased intercellular CO_2 concentration), higher non-photochemistry efficiency [increased non-photochemical quenching values (NPQ)], and higher photochemistry efficiency [increased the maximum quantum yield in the dark-adapted state (Fv/Fm), the maximum quantum yield in the light-adapted sate (Fv′/Fm′), the actual quantum yield in the light-adapted steady state (φPSII) and the photochemical quenching values (qP)], compared with non-mycorrhizal maize plants. In addition, AM symbiosis could trigger the regulation of the energy biturcation between photochemical and non-photochemical events reflected in the deexcitation rate constants (kN, kN′, kP, and kP′). All the results show that *G. mosseae* alleviates the deleterious effect of salt stress on plant growth, through improving plant water status, chlorophyll concentration, and photosynthetic capacity, while the influence of AM symbiosis on photosynthetic capacity of maize plants can be indirectly affected by soil salinity and mycorrhizae-mediated enhancement of water status, but not by the mycorrhizae-mediated enhancement of chlorophyll concentration and plant biomass.

Keywords Arbuscular mycorrhiza · Chlorophyll fluorescence · Gas exchange · Salt stress · Water status · *Zea*

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Introduction

Soil salinization is a widespread problem. Approximately 7% of the global land surface is covered with saline soil (Ruiz-Lozano et al. 1996). Out of 1.5 billion ha cultivated land, about 77 million ha (5%) are affected by excess salt content mainly induced by irrigation with ground water of high salt content (Munns et al. 1999). These problem soils also occur in China, where it was estimated that about 3,693 hm^2 land was saline (Zhao and Li 1999). It is well known that crop production is low in saline soil, mainly due to salt toxicity to plants leading to a decrease in plant water-holding capacity, the imbalance of nutrient uptake, and toxicity of ions towards plant photosynthesis (Katerji et al. 1998; van Hoorn et al. 2001).

AM fungi widely occur in salt stress environments (Wang and Liu 2001; Rozema et al. 1986). Recently, many researchers reported that AM fungi could enhance the

ability of plants to cope with salt stress (Yano-Melo et al. 2003; Rabie 2005; Jahromi et al. 2008) by improving plant nutrient uptake (Cantrell and Linderman 2001; Asghari et al. 2005) and ion balance (Zandavalli et al. 2004; Giri et al. 2007), protecting enzyme activity (Rabie and Almadini 2005; Giri and Mukerji 2004), and facilitating water uptake (Berta et al. 1990; Ruiz-Lozano and Azcón 1995). Shi et al. (2002) and Shi and Guo (2006) found that salt stress could decrease photosynthetic ability and induce physiological drought in plants, which leads to a decrease in crop production. However, there have been very few attempts to study the influence of AM inoculum on photosynthesis and water status under salt stress. Only a few reports have indicated that AM colonization could enhance relative water content in zucchini leaves (Colla et al. 2008), water potential of maize plants (Feng et al. 2000a), and chlorophyll concentration in the leaves of several plant species, i.e., *Sesbania aegyptiaca*, *Sesbania grandiflora*, and *Lotus glaber* (Giri and Mukerji 2004; Sannazzaro et al. 2006; Colla et al. 2008).

The objective of this study was to define the effect of an established AM association on plant water status, chlorophyll, gas exchange, and chlorophyll fluorescence of maize leaves in order to improve understanding of the mechanisms regarding the alleviation of salt toxicity in AM plants.

Materials and methods

Plant and soil treatment

The soil used in this study was collected from the top layer (0–20 cm) of a soil in Yangling City, Shaanxi Province, China. The soil (pH 7.6, soil/water ratio of 1:2.5 *w*/*v*), containing 20 g/kg organic matter, 37 mg/kg available nitrogen, 12 mg/kg available phosphorus, and 207 mg/kg available potassium measured according to the method described by Bao (2000), was subsequently ground, sieved through a 2-mm sieve, and mixed with fine sand (sand/soil, 1:2 *v*/*v*). The mixture was autoclaved at 121°C for 2 h.

Maize seeds, whose cultivar name is Shandan 16, supplied by the College of Agriculture, Northwest A&F University, Yangling City, Shaanxi Province, China, were surface-sterilized with 0.1% $HgCl_2$ for 3 min and then washed five times with sterile distilled water. Thereafter, seeds were arranged on sterilized moist filter paper to allow germination at 28°C. Pre-germinated seeds were sown at a rate of five per pot (150 mm height × 150 mm diameter) containing 2 kg of autoclaved sand and soil mixture. Seedlings were thinned to two seedlings per pot 10 days after sowing. The plants were supplemented with a nutrient solution of the following composition: KNO_3 6 mM, $NH_4H_2PO_4$ 1 mM, $MgSO_4$ 2.6 mM, $Ca(NO_3)_2$ 8 mM, H_3BO_3 10 μM, $MnSO_4$ 1.6 μM, $ZnSO_4$ 1.0 μM, $CuSO_4$ 0.5 μM, $(NH_4)_6Mo_2O_4$ 50 μM, and Fe-EDTA 20 μM. The solution pH was adjusted to 6.5±0.3.

AM inoculum

Mycorrhizal inoculum consisted of soil, spores (the spore density was 306–420 per 100 g dry soil) and mycelium of *Glomus mosseae* (Nicolson & Gerdemann), and infected root fragments with an infection level of 94%. *G. mosseae* was initially isolated from a saline soil in Inner Mongolia Autonomous Region, China and multiplied in pot cultures using *Zea mays* L. as host. Each pot was inoculated with 30 g inoculum for mycorrhizal treatment or 30 g sterilized inoculum plus 10 ml mycorrhizal fungi-free filtrate meshing from the inoculum suspension as the non-mycorrhizal treatment. Half of the pots received live *G. mosseae* by placing mycorrhizal inoculum in soil below the maize seeds prior to sowing.

Experimental design

The experiment was conducted in a greenhouse under a temperature of 22–30°C, 12–14 h day light, and 70–75% relative humidity, between July and September 2006. This experiment was arranged in a randomized block design. Treatments were factorial combinations of two factors: (1) non-mycorrhizal control and *G. mosseae* as a mycorrhizal inoculum and (2) five NaCl levels of 0, 0.5, 1.0, 1.5, and 2.0 g/kg dry substrate, respectively. The maize plants were grown for 15 days before being exposed to the five NaCl levels, achieved by adding NaCl in irrigation water (0, 10, 20, 30, and 40 g/l), in order to avoid salt effects on AM establishment and on fine maize seedlings. To avoid osmotic shock, NaCl was introduced gradually by successively adding 20 ml of the prescribed NaCl solutions in each pot each day for 5 days starting at day 15 after sowing. A total amount of 100 ml of the corresponding saline solution was added per pot in this experiment. Five pots per treatment were used and the plants were harvested 70 days after sowing.

Measurements and analysis

Root and shoot biomass were determined after oven drying at 70°C for 90 h. Relative water content and water saturation deficit were measured according to the method described by Gao (2000).

Relative chlorophyll concentration was measured on the second fully expanded leaf using CM-1000 chlorophyll meter (Spectrum, USA) according to the manufacturer's instructions. Gas exchange parameters (including net

photosynthetic rate, stomatal conductance, intercellular CO_2 concentration, and transpiration rate) were determined using a portable open flow gas exchange system LI-6400 (LI-COR, USA) from 08:30 to 11:30 A.M. The photosynthetically active radiation was 1,000±12 μmol m^{-2} s^{-1}, CO_2 concentration 350±2 cm^3 m^{-3}, leaf temperature 28.0±0.8°C, and flow rate of atmosphere 0.5 dm^3 min^{-1}. Water use efficiency was calculated as the ratio of net photosynthetic rate per transpiration rate. Chlorophyll fluorescence was measured on the second fully expanded leaf at room temperature using LI-6400-40 fluorometer (LI-COR, USA) based on the principle of Feng et al. (2001). After darkening the leaves for 30 min, the minimal fluorescence in the dark-adapted state (Fo) was recorded and a saturating pulse of radiation (5,000 μmol m^{-2} s^{-1}) was given for 0.7 s to determine the maximal fluorescence in the dark-adapted state (Fm). Then, the leaves were irradiated with actinic light (400 μmol m^{-2} s^{-1}) for 150 s to measure the steady-state fluorescence in the light (Fs′). Afterwards, a radiation (5,000 μmol m^{-2} s^{-1}) was given for 0.7 s to determine the maximal fluorescence yields in the light-adapted state (Fm′). Following this, the actinic radiation was turned off for a period of 3 s, and a far-red radiation was turned on for a period of 5 s to reoxidize the photosystem II (PSII) centers and measure the minimal fluorescence in the dark with a non-photochemical quenching similar to that found at steady state under irradiation (Fo′). We calculated the maximum quantum yield in the dark-adapted state (Fv/Fm), the maximum quantum yield in the light-adapted sate (Fv′/Fm′), the actual quantum yield in the light-adapted steady state (φPSII), the photochemical quenching values (qP), the non-photochemical quenching values (NPQ), and the deexcitation rate constant such as kN, kP in the dark and kN′, and kP′ in the light-adapted state according to the following equations:

$$\mathrm{NPQ} = \frac{\mathrm{Fm}}{\mathrm{Fm'}} - 1; \mathrm{qP} = \frac{(\mathrm{Fm'} - \mathrm{Fs'})}{(\mathrm{Fm'} - \mathrm{Fo'})}; \mathrm{Fv/Fm} = 1 - \frac{\mathrm{Fo}}{\mathrm{Fm}}; \mathrm{Fv'/Fm'} = 1 - \frac{\mathrm{Fo'}}{\mathrm{Fm'}}; \varphi\mathrm{PSII} = 1 - \frac{\mathrm{Fs'}}{\mathrm{Fm'}};$$

$$\mathrm{kN} = \frac{1}{\mathrm{Fm}}; \mathrm{kN'} = \frac{1}{\mathrm{Fm'}}; \mathrm{kP} = \frac{1}{\mathrm{Fo}} - \frac{1}{\mathrm{Fm}}; \mathrm{kP'} = \frac{1}{\mathrm{Fo'}} - \frac{1}{\mathrm{Fm'}}.$$

To identify the AM colonization rate, roots were collected and washed gently under running tap water, and rinsed with distilled water. A subsample of 0.5 g root segments was cut into 1-cm-long segments, cleared 15 min in 10% KOH at 90°C, bleached in alkaline hydrogen peroxide for 20 min, acidified in 1% HCl, and stained in lactophenol blue (Phillings and Hayman 1970). Colonization rate was measured using the gridline intercept method described by Giovannetti and Mosse (1980).

Statistical analysis

The data were subjected to correlation analysis and two-way analysis of variance using ANOVA, means were compared by Duncan's test at the 5% level (SAS version 8.0).

Results

Plant growth and AM fungal colonization

The symptom of salt injury, leaves becoming yellow and sapless, was observed in the leaves of plants treated with 1.5 and 2.0 g/kg NaCl levels. Plant injury at 2.0 g/kg NaCl was more severe than at 1.5 g/kg NaCl, and injury was more severe in non-mycorrhizal plants than mycorrhizal plants at the same NaCl level through observing the yellow or sapless degree of plant leaves.

None of the maize plants in the non-inoculated treatments was colonized by *G. mosseae*. Plants inoculated with *G. mosseae* had AM fungal root colonization of 99–79%. The highest AM root colonization level was in salt-free soil, the lowest was in the presence of 2.0 g/kg NaCl (Table 1). There was significantly a negative correlation between AM fungal root colonization and salinity (r=−0.94, p<0.05), which means salinity suppresses AM establishment.

Dry weight of shoot and root was higher in mycorrhizal than non-mycorrhizal plants regardless of salinity level and decreased while soil salinity increased. However, no significant difference in shoot dry weight was recorded between mycorrhizal and non-mycorrhizal plants in the high salinity (2.0 g/kg NaCl) treatment (Table 1).

Water status

Relative water content in the leaves was higher in mycorrhizal than non-mycorrhizal plants at all salinity levels, although the difference was not significant in the 0 g/kg NaCl treatment (Fig. 1a). Water saturation deficit in the leaves was lower in mycorrhizal than non-mycorrhizal plants grown at all salinity levels, but no significant differences were observed at all salinity levels (Fig. 1b). Water use efficiency decreased with increasing salinity in both mycorrhizal and non-mycorrhizal plant leaves. At 2.0 g/kg NaCl level, only 4 and 2 μmol CO_2 $mmol^{-1}$ H_2O were recorded in the leaves of mycorrhizal and non-mycorrhizal plants, respectively. The colonization by *G. mosseae* significantly enhanced water use efficiency by 61–206% (Fig. 1c).

Table 1 Arbuscular mycorrhizal root colonization (RC), and dry weight of shoot and root of maize plants inoculated (+M) or not (−M) with *Glomus mosseae* at five NaCl levels

NaCl level (g/kg)	Inoculation	RC (%)	Shoot dry weight (g/pot)	Root dry weight (g/pot)
0	+M	99a	6.15±0.86a	2.37±0.20a
	−M		3.07±0.57b	1.32±0.21c
0.5	+M	98a	5.55±0.95a	2.26±0.49a
	−M		2.90±0.39b	1.20±0.04cd
1.0	+M	95a	3.69±1.00b	1.65±0.17b
	−M		1.43±0.45c	1.09±0.19cde
1.5	+M	82ab	3.57±0.90b	1.24±0.01cd
	−M		1.38±0.33c	0.87±0.02ef
2.0	+M	79b	1.76±0.11c	0.94±0.05ed
	−M		0.83±0.13c	0.60±0.02f

Means (±SD) labeled with different letters within each column are significantly different ($p<0.05$) by Duncan's test; $n=5$

Chlorophyll

At all salinity levels, plants colonized by *G. mosseae* had higher relative chlorophyll concentration compared with non-mycorrhizal plants. These significant differences in relative chlorophyll concentration were recorded between mycorrhizal and non-mycorrhizal plants grown at the salinity levels of 0, 0.5, 1.0, and 1.5 g/kg NaCl. Relative chlorophyll concentration in the leaves of both AM-inoculated and non-inoculated plants decreased as soil salinity increased (Fig. 1d).

Gas exchange

Root colonization by *G. mosseae* enhanced net photosynthetic rate (by 66–1,615%) and stomatal conductance (by 14%–853%) and reduced intercellular CO_2 concentration (by 77–89%) of the leaves of maize plants grown at all salinity levels (Fig. 2a–c). With increasing salinity, net photosynthetic rate and stomatal conductance in both AM-inoculated and non-inoculated maize leaves first show an increasing and then, a decreasing trend (Fig. 2a,b). Intercellular CO_2 concentration increased with salinity

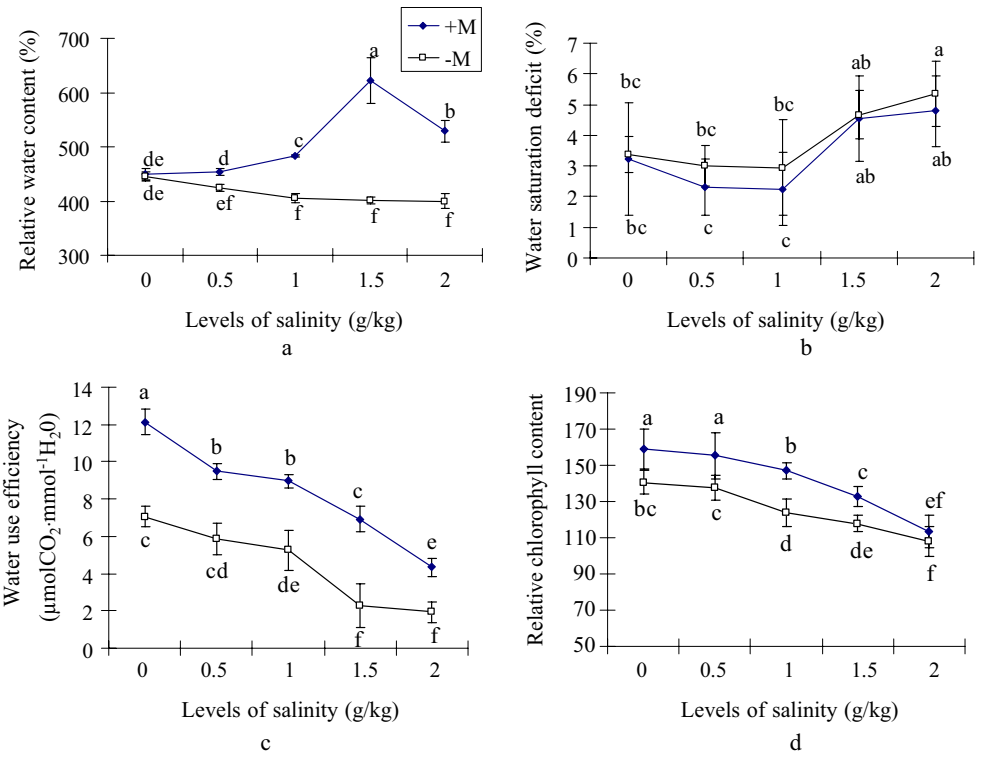

Fig. 1 a–d Influence of *Glomus mosseae* on relative water content, water saturation deficit, water use efficiency, and relative chlorophyll concentration in the leaves of maize plants inoculated (+M) or not (−M) with *G. mosseae* at five NaCl levels. Mean pairs followed by *different letters* are significantly different ($p<0.05$) by Duncan's test; $n=5$

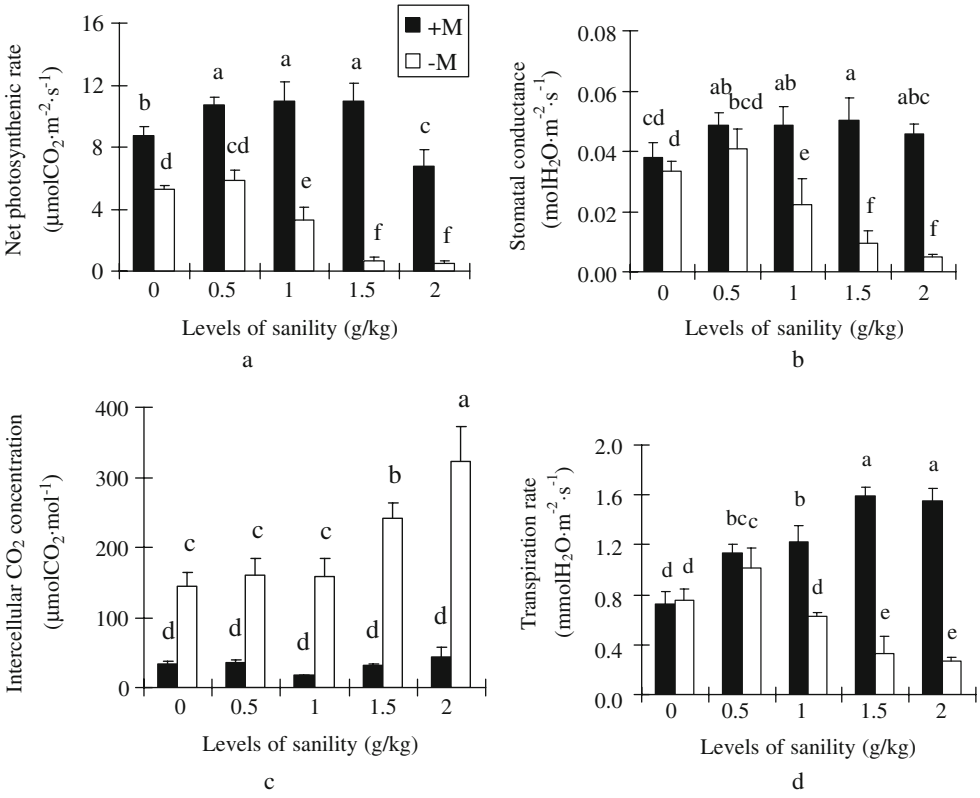

Fig. 2 **a–d** Influence of *Glomus mosseae* on net photosynthetic rate, stomatal conductance, intercellular CO_2 concentration, and transpiration rate in the leaves of maize plants inoculated (+M) or not (−M) with *G. mosseae* at five NaCl levels. Mean pairs followed by *different letters* are significantly different ($p<0.05$) by Duncan's test; $n=5$

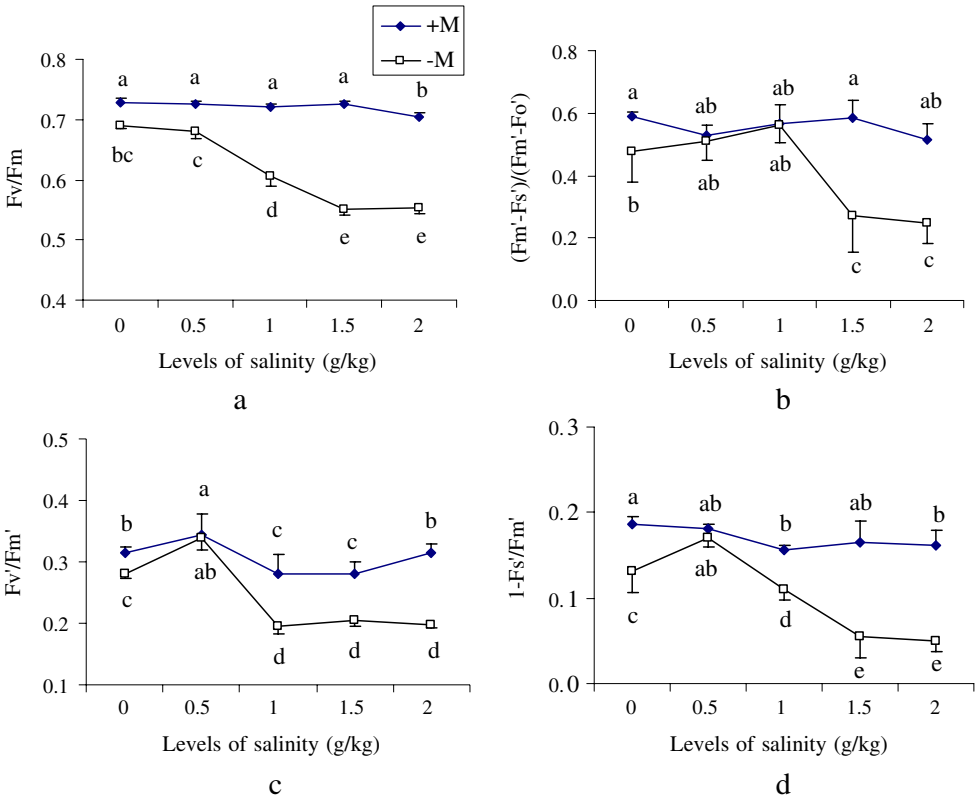

Fig. 3 **a–d** Influence of *Glomus mosseae* on the photochemical quenching values (qP), the maximum quantum yield in the dark-adapted state (Fv/Fm), the maximum quantum yield in the light-adapted state (Fv′/Fm′), and the actual quantum yield in light-adapted steady state (φPSII) in the leaves of maize plants inoculated (+M) or not (−M) with *G. mosseae* at five NaCl levels. Mean pairs followed by *different letters* are significantly different ($p<0.05$) by Duncan's test; $n=5$

(Fig. 2c). At 0 and 0.5 g/kg NaCl levels, the transpiration rate in mycorrhizal and non-mycorrhizal plants was similar. However, At 1.0, 1.5, and 2.0 g/kg NaCl levels, the transpiration rate of mycorrhizal plants, respectively, increased by 95%, 382%, and 477% compared with the corresponding controls (Fig. 2d).

Chlorophyll fluorescence

AM symbiosis increased the parameters of Fv/Fm, Fv′/Fm′, φPSII, and qP compared with non-mycorrhizal plants regardless of salinity levels (Fig. 3a–d). The non-photochemical quenching parameter NPQ were higher for mycorrhizal than for non-mycorrhizal plants at all NaCl levels (Fig. 4). At 0, 0.5, and 1.0 g/kg NaCl levels, the Fo of mycorrhizal plants was significantly lower than that of non-mycorrhizal plants, whereas at 1.5 and 2.0 g/kg NaCl levels, there were no significant differences in Fo between mycorrhizal and non-mycorrhizal plants (Table 2). In the presence of NaCl, Fm, Fm′, Fo′, and Fs′ of mycorrhizal plants were higher than that of non-mycorrhizal plants (Table 2). In the dark- or light-adapted state, mycorrhizal plants had higher kP or kP′ and lower kN or kN′ compared with non-mycorrhizal plants regardless of salinity levels (Fig. 5a–b). At 0, 0.5, and 1.0 g/kg NaCl levels, the sum of all deexcitation rate constants (kN+kP) in the dark-adapted state were significantly higher for mycorrhizal than for non-mycorrhizal plants, whereas at 1.5 and 2.0 g/kg NaCl levels, there were no significant differences in kN+kP between mycorrhizal and non-mycorrhizal plants (Fig. 5a). At 1.5 and 2.0 g/kg NaCl levels, the sum of all deexcitation rate constants (kN′+kP′) in the light-adapted state was significantly higher for non-mycorrhizal than for mycorrhizal plants, whereas at 0, 0.5 and 1.0 g/kg NaCl levels, there were no significant differences in kN′+kP′ between mycorrhizal and non-mycorrhizal plants (Fig. 5b).

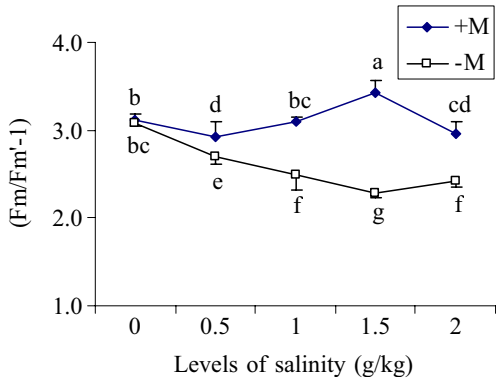

Fig. 4 Influence of *Glomus mosseae* on the non-photochemical quenching values (NPQ) in the leaves of maize plants inoculated (+M) or not (−M) with *G. mosseae* at five NaCl levels. Mean pairs followed by *different letters* are significantly different ($p<0.05$) by Duncan's test; $n=5$

Discussion

Mycorrhizal symbiosis is a key component in helping plants survive under adverse environmental conditions (Augé et al. 1992). Our results showed that maize plants inoculated with *G. mosseae* had higher shoot and root dry weight than non-mycorrhizal plants when being exposed to salt stress, which means mycorrhizal plants grow better than non-mycorrhizal plants under saline conditions. This is in agreement with many greenhouse studies on tomato (Al-Karaki and Hammad 2001), cotton (Feng and Zhang 2003), barley (Mohammad et al. 2003), and maize (Feng et al. 2000b). In addition, Rosendahl and Rosendahl (1991) have pointed out that soil salinity could affect the enhancement of plant growth induced by AM symbiosis. However, the data of this study showed that there was no significant correlation between salinity and the enhancement (mycorrhizal plants/non-mycorrhizal plants) of shoot dry weight ($r=-0.76$, $p>0.05$) and root dry weight ($r=-0.44$, $p>0.05$). This may be induced by different salinities and plant species used in different researches.

Many stressful conditions, such as aridity, salinity, and high or low temperature, could disrupt components of plant's photosynthetic apparatus, such as membrane integrity, and further decrease photosynthetic capacity (Powles 1984; Demmig-Adams and Adams 1992). In this study, phenomenologically the gas exchange data showed very nicely that the optimum for NaCl for gas exchange activities was at a salinity of about 0.5 g/kg without mycorrhiza and in the presence of mycorrhiza about at 1.5 g/kg. This is a very important stress buffer effect due to the symbiosis with mycorrhiza. In the presence of mycorrhizae, maize plants had higher stomatal conductance, higher transpiration rate, higher net photosynthetic rate, and lower intercellular CO_2 concentration compared with that of non-mycorrhizal plants under salt stress. Normally, the higher intercellular CO_2 concentration is beneficial for photosynthesis, but, under salt stress, an increase in intercellular CO_2 concentration indirectly indicates the destruction of photosynthetic apparatus since a decrease in stomatal conductance (Powles 1984) and the passivation of the enzyme (Munns 2002) induced by salt stress can induce CO_2 to accumulate in intercellular areas. Thus, we could say that AM fungal colonization can elevate the photosynthetic ability through improving the gas exchange capacity of maize plants under salt stress.

Another method in studying plant photosynthesis is chlorophyll fluorescence analysis, which has become one of the most powerful and widely used techniques. The principle of chlorophyll fluorescence analysis is relatively straightforward. Light energy absorbed by chlorophyll molecules in a leaf can undergo one of three fates: it can be used to drive photosynthesis (photochemistry), excess

Table 2 Influence of *Glomus mosseae* on the minimal fluorescence in the dark-adapted state (Fo), the maximal fluorescence in the dark-adapted state (Fm), the steady-state fluorescence in the light (Fs′), the maximal fluorescence yields in light-adapted state (Fm′), and the minimal fluorescence in the dark with a non-photochemical quenching similar to that found at steady state under irradiation (Fo′) in the leaves of maize plants inoculated (+M) or not (−M) with *G. mosseae* at five NaCl levels

NaCl level (g/kg)	Inoculation	Fm	Fo	Fo′	Fm′	Fs′
0	+M	474.15±1.37c	128.77±3.05e	78.91±0.31bcd	115.05±1.96cd	93.67±0.55cd
	−M	459.33±1.14d	140.57±2.43abc	81.20±0.93b	112.48±0.66d	97.62±3.52ab
0.5	+M	475.63±5.44c	130.35±1.53e	79.64±1.53bc	121.63±7.15a	99.67±5.03a
	−M	436.12±2.54e	138.07±4.92bcd	78.02±1.66cd	117.93±2.92abc	97.75±3.60ab
1.0	+M	490.59±2.85b	136.34±0.99d	86.27±3.76a	119.80±1.38ab	101.04±0.59a
	−M	366.45±17.48f	143.77±2.88a	84.46±1.43a	105.04±0.18e	93.54±1.31cd
1.5	+M	518.57±0.82a	141.79±1.95ab	84.27±0.35a	117.05±3.53bc	97.70±1.12ab
	−M	315.80±3.99g	141.70±2.00ab	76.75±0.99d	96.39±0.31f	91.02±2.73d
2.0	+M	452.74±12.14d	134.38±1.26d	78.61±2.31cd	114.51±2.55cd	96.08±0.34bc
	−M	307.57±3.97g	137.40±4.34cd	72.09±1.68e	89.89±1.64g	85.47±0.69e

Means (±SD) labeled with different letters within each column are significantly different ($p<0.05$) by Duncan's test; $n=5$.

energy can be dissipated as heat, or it can be re-emitted as light-chlorophyll fluorescence (non-photochemistry). In the brief history of chlorophyll fluorescence analysis, a large number of different coefficients have been calculated to quantify photochemical and non-photochemical quenching. Broadly, Fv/Fm, Fv′/Fm′, φPSII, and qP have been called photochemical quenching parameters, and NPQ is a non-photochemical quenching parameter (Maxwell and Johnson 2000; Havaux et al. 1991). The ratio of Fv/Fm is a measure of the capacity of the primary photochemistry of PSII, which itself is particularly sensitive to a variety of environmental stress-inducing factors. It has been shown to be a reliable indicator of stress (Krause and Weis 1991; Figueroa et al. 1997). The results of this study pointed out that Fv/Fm in the leaves of mycorrhizal plants were significantly higher than that in non-mycorrhizal plants. This, together with higher Fv′/Fm′, φPSII, and qP in the leaves of mycorrhizal plants, implies that the efficiency of PSII photochemistry of mycorrhizal plants is higher than that of non-mycorrhizal plants. With regard to the influence of AM mycorrhizae on the non-photochemical processes, the data of this study showed that AM-inoculated plants had higher NPQ than non-inoculated plants. As we know, NPQ quantify the non-photochemical quenching (Maxwell and Johnson 2000). Any change in NPQ measures a change in the efficiency of heat dissipation, relative to the dark-adapted state. Broadly, an increase in NPQ can occur as a result of processes that protect the leaf from light-induced damage (Maxwell and Johnson 2000). Hence, we can say that AM-inoculated plants have higher ability to protect leaves from light-induced damage. In addition, our data pointed out the rising trend in Fo with increasing salinity recorded in the leaves of both mycorrhizal and non-mycorrhizal plants, but Fo was lower in the leaves of mycorrhizal plants than non-mycorrhizal plants at most NaCl levels. Fo measures the minimal fluorescence in the dark-adapted state. An increase in Fo due to stressful conditions indicates the destruction or malfunction of PSII reaction center, or disruption of electron transport for excitation of reaction centers (Araus et al. 1998; Bolhar-Nordenkampf et al. 1989). Hence, our results suggest that salt stress could destroy PSII reaction center or disrupt electron transport in photosynthetic apparatus of both mycorrhizal and non-mycorrhizal plants, whereas the toxic influence of salinity on PSII reaction center could be mitigated by AM symbiosis.

The fluorescence parameters (kP, kP′, kN, kN′) can be used as qualitative indicators of the individual rate constants, allowing to monitor the general trends in the energy dissipation adjustments in PSII (Havaux et al. 1991; Paillotin 1976). In the dark- or light-adapted state, mycorrhizal plants had higher kP or kP′ and lower kN or kN′ compared with non-mycorrhizal plants. This shows that the effect of AM symbiosis on the physical deexcitation rate constant is qualitatively and quantitatively very similar in the dark- and the light-adapted states, and AM symbiosis triggers the regulation of the energy bifurcation between photochemical and non-photochemical events, which forms the basis for further investigations where with fast direct fluorescence techniques the site of actions of the mycorrhizal effect can be localized within the energy cascade from light absorption to the reduction of NADP.

We found that AM symbiosis improves the photosynthetic capacity of maize leaves, mainly through elevating the capacity of gas exchange and the efficiency of photochemistry and non-photochemistry of PSII and regulating the energy bifurcation between photochemical and non-photochemical events, while it is essential to point out that the favorable effect of AM symbiosis on the gas exchange activity and chlorophyll fluorescence of maize plants occurred not only under salt stress, but also in absence of salt stress. This, together with the significant association between soil salinity and the AM-

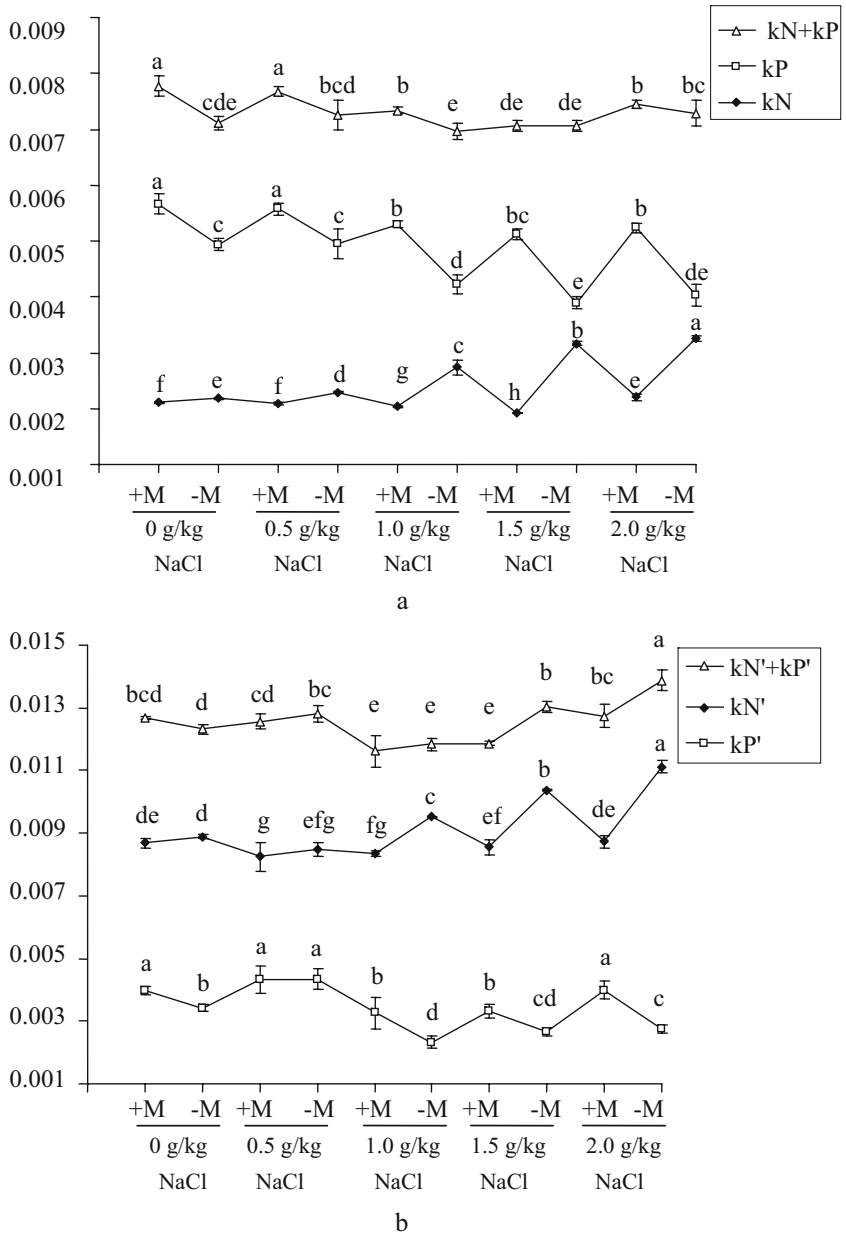

Fig. 5 a–b Influence of *Glomus mosseae* on the physical deexcitation rate constant (kN, kN′, kP, kP′) and the sum of all deexcitation rate constants (kN+kP, kN′+kP′) in the leaves of maize plants inoculated (+M) or not (−M) with *G. mosseae* at five NaCl levels. Mean pairs followed by different letters are significantly different ($p<0.05$) by Duncan's test; $n=5$

related change (mycorrhizal plants/non-mycorrhizal plants) of Fo ($r=0.89$, $p<0.05$), Fm ($r=0.88$, $p<0.05$), Fo′ ($r=0.93$, $p<0.05$), Fm′ ($r=0.98$, $p<0.01$), Fs′ ($r=0.95$, $p<0.05$), Fv/Fm ($r=0.91$, $p<0.05$), φPSII ($r=0.88$, $p<0.05$), stomatal conductance ($r=0.92$, $p<0.05$), transpiration rate ($r=0.95$, $p<0.05$), kN ($r=-0.91$, $p<0.05$), kP ($r=0.89$, $p<0.05$), kN+kP ($r=-0.88$, $p<0.05$), kN′ ($r=-0.98$, $p<0.01$), and kN′+kP′ ($r=-0.94$, $p<0.05$), suggests that this change is not a specific process induced by salt stress; however, the AM-related change in photosynthetic capacity was related with soil salinity. The change in photosynthetic capacity is not simply induced by changes in plant size via AM symbiosis since the change degree (mycorrhizal plants/non-mycorrhizal plants) of plant biomass had no significant correlation with the change degree (mycorrhizal plants/non-mycorrhizal plants) of gas exchange parameters, water status, and fluorescence parameters.

Our results indicated that the AM symbiosis could enhance the chlorophyll concentration of maize leaves, which is in agreement with the results of other studies (Giri and Mukerji 2004; Sannazzaro et al. 2006; Colla et al. 2008). This, together with no significant association between the enhancement (mycorrhizal plants/non-mycorrhizal plants) of relative chlorophyll concentration and the improvement (mycorrhizal plants/non-mycorrhizal plants) of gas exchange and chlorophyll fluorescence parameters via AM symbiosis, suggests that the mycorrhizae-mediated increase in chlorophyll fluorescence parameters and in gas exchange param-

eters is not related with mycorrhizae-mediated improvement of chlorophyll concentration.

In addition, the result of this study clearly shows that the AM symbiosis can improve plant water status. Mycorrhizal plant leaves had higher relative water content, higher water use efficiency, and lower water saturation deficit in the presence of NaCl. As we know, better water status is beneficial for plant growth. The better growth recorded in mycorrhizal plants may be partly attributed to their better water status. This is in agreement with the results of others (Feng et al. 2000a; Colla et al. 2008). Furthermore, the improvement of water status via AM symbiosis could play an indirect role in enhancing the capacity of gas exchange and the efficiency of photochemistry and non-photochemistry of PSII, and changing the physical deexcitation rate constant since the change degree (mycorrhizal plants/non-mycorrhizal plants) of relative water content significantly correlated with the change degree (mycorrhizal plants/non-mycorrhizal plants) of Fm (r=0.98, p<0.01), Fo′ (r=0.92, p<0.05), NPQ (r=0.97, p<0.01), qP (r=0.85, p<0.05), Fv/Fm (r=0.96, p<0.01), net photosynthetic rate (r=0.95, p<0.05), transpiration rate (r=0.85, p<0.05), kN (r=−0.95, p<0.05), kP (r=0.90, p<0.05), kN+kP (r=−0.96, p<0.01), and kN′+kP′ (r=−0.91, p<0.05). The enhancement of water status via AM symbiosis was related to improved water uptake contributed by AM fungal hypha (Jiang and Huang 2003), changes in root structure, and enhanced root activity due to the colonization of AM fungi (Berta et al. 1990).

In conclusion, AM fungi can protect plants against salt stress. However, it is not very clear how the AM symbiosis affects chlorophyll, gas exchange, and chlorophyll fluorescence in plant leaves. Thus, it is necessary to conduct further studies on the mechanism by which the AM symbiosis influences chlorophyll concentration, gas exchange, and chlorophyll fluorescence of plant leaves.

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