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Arbuscular Mycorrhizal Fungi Alleviate the Negative Effect of Temperature Stress in Millet Lines with Contrasting Soil Aggregation Potential

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Abstract

Arbuscular mycorrhizal fungi (AMF) establish a mutualistic symbiosis with several plants and play a key role in improving plant growth, tolerance to abiotic and biotic stresses as well as the soil structure. This work aimed at elucidating the AMF temperature stress modulating impact on four pearl millet lines plant growth and soil aggregation. Experimental trials were carried out in both greenhouse and growth chamber to determine the response of the four millet lines to inoculation with two AMF strains (*Rhizophagus aggregatus* and *Funneliformis mosseae*) under heat and non-stress conditions. We first investigated the mycorrhizal colonization (MC) and the mycorrhizal growth response (MGR) of millet lines in relation with their soil aggregation potential (root adhering soil/root biomass, MAS/RB) in the greenhouse. Secondly, the four millet lines were grown in two separated growth chambers and subjected to a day/night temperature of 32/28 °C as the control treatment and 37/32 °C as the temperature stress treatment. Plant growth, mycorrhization rate and several physiological, mycorrhizal and soil parameters were measured. Results showed that the mycorrhization rates of millet lines were low and not significantly different. *Funneliformis mosseae* (31.39%) showed higher root colonization than *Rhizophagus aggregatus* (22.79%) and control (9.79%). The temperature stress reduced the mycorrhizal colonization rate, shoot and root biomass, and the soil aggregation for all tested lines. L220 and L132 showed more MC rate and MGR than the other lines under control and high-temperature treatment. The MGR was significantly better under temperature stress conditions than in the control. Under the temperature stress conditions, inoculation with *R. aggregatus* and *F. mosseae* increased chlorophyll concentration, root dry weight and shoot dry weight as compared to non-inoculated plants. AMF inoculation, particularly with *F. mosseae* had a positive influence on the tolerance of millet lines to temperature stress. This study demonstrates that AMF play an important role in the response of these four millet lines to temperature stress. AMF is therefore an important component in the adaptation of crops to climatic variations in Sub-Saharan Africa.

Keywords Arbuscular mycorrhizal fungi · Temperature stress · Stress tolerance · Pearl millet lines · Soil aggregation

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Arbuskuläre Mykorrhizapilze mildern die negativen Auswirkungen von Temperaturstress bei Hirsesorten mit unterschiedlichem Bodenaggregationspotenzial

Zusammenfassung

Arbuskuläre Mykorrhizapilze (AMF) gehen mit verschiedenen Pflanzen eine wechselseitige Symbiose ein und spielen eine Schlüsselrolle bei der Verbesserung des Pflanzenwachstums, der Toleranz gegenüber abiotischen und biotischen Stressfaktoren sowie der Bodenstruktur. Ziel dieser Arbeit war es, den Einfluss von AMF auf das Pflanzenwachstum und die Bodenaggregation von vier Perlhirse-Linien zu untersuchen. Experimentelle Versuche wurden sowohl im Gewächshaus als auch in der Wachstumskammer durchgeführt, um die Reaktion der vier Hirsesorten auf die Inokulation mit zwei AMF-Stämmen (*Rhizophagus aggregatus* und *Funneliformis mosseae*) unter Hitze- und Nichtstressbedingungen zu bestimmen. Zunächst untersuchten wir im Gewächshaus die Mykorrhizabesiedlung (MC) und die Mykorrhizawachstumsreaktion (MGR) der Hirsesorten in Abhängigkeit von ihrem Bodenaggregationspotenzial (Wurzelanhaftung/Wurzelbiomasse, MAS/RB). Im Anschluss wurden die vier Hirsesorten in zwei getrennten Wachstumskammern angebaut und einer Tages-/Nachttemperatur von 32/28 °C als Kontrollbehandlung und 37/32 °C als Temperaturstressbehandlung unterzogen. Das Pflanzenwachstum, die Mykorrhizierungsrate und verschiedene physiologische, Mykorrhizierungs- und Bodenparameter wurden gemessen. Die Ergebnisse zeigten, dass die Mykorrhizierungsraten der Hirsesorten niedrig waren und sich nicht signifikant unterschieden. *Funneliformis mosseae* (31,39 %) zeigte eine höhere Wurzelbesiedlung als *Rhizophagus aggregatus* (22,79 %) und die Kontrolle (9,79 %). Der Temperaturstress reduziert die Mykorrhizabesiedlungsrate, die Spross- und Wurzelbiomasse sowie die Bodenaggregation bei allen getesteten Linien. L220 und L132 zeigten eine höhere MC-Rate und MGR als die anderen Linien unter der Kontroll- und Hochtemperaturbehandlung. Die MGR war unter Temperaturstressbedingungen signifikant besser als in der Kontrollgruppe. Unter den Temperaturstressbedingungen erhöhte die Inokulation mit *R. aggregatus* und *F. mosseae* die Chlorophyllkonzentration, das Wurzeltrockengewicht und das Sprossen-Trockengewicht im Vergleich zu nicht inokulierten Pflanzen. Die Beimpfung mit AMF, insbesondere mit *F. mosseae*, hatte einen positiven Einfluss auf die Toleranz der Hirsepflanzen gegenüber Temperaturstress. Diese Studie zeigt, dass AMF eine wichtige Rolle bei der Reaktion dieser vier Hirsesorten auf Temperaturstress spielen. AMF ist daher eine wichtige Komponente bei der Anpassung von Nutzpflanzen an Klimaschwankungen in Afrika südlich der Sahara.

Schlüsselwörter Arbuskuläre Mykorrhiza-Pilze · Temperaturbelastung · Stresstoleranz · Perlhirse-Linien

Introduction

In Sub-Saharan Africa, cereal crops play a crucial role in ensuring food security (Gaye 1994). Millet (*Pennisetum glaucum L. R. Br.*) is one of the cereals grown in the arid and semi-arid zones of Africa and Asia (FAO, 2009). In Senegal, it is the most cultivated cereal, occupying ~71% of the land allocated to cereals, and accounts for ~60% of total cereal production. However, despite the country's agricultural potential, millet productivity is still low (Kane et al. 2016). This low productivity is associated with agricultural land degradation (Traoré and Bagayogo 2002), reduced fallow duration and the crop monoculture practice (Bationo et al. 1993; Samaké et al. 2005). These factors result in a decreased soil fertility, and thus, low productivity (Buresh et al., 1997). Faced with this problem, sustainable management of soil fertility is essential to increase millet yields (Gaston et al. 2016; Naoura et al. 2014).

The symbiotic association between plants and soil microorganisms plays an important role in improving plant growth and increasing the productivity of agrosystems (Dirlewanger et al. 2002). In addition to ecosystem functions, soil microorganisms are also involved in improving soil structure through the formation and stabilization of aggregates (Bethlenfalvay and Barea 2009; Rillig and Mummey 2006). The role of soil microorganisms in the soil aggregation process is influenced by plant species and activities through root architecture and rhizodeposition (Bronick and Lal 2005). However, the quantity and quality of exudates produced depend on the photosynthetic activity, the genotype and the plant growth stage (Aulakh et al. 2001). Besides, Chaney and Swift (1984) showed that plant roots and fungal mycelium are actively involved in the soil aggregation process. Alone, they control ~40% of soil aggregation.

The influence of plants on soil microbial activity and soil aggregation has been widely documented on maize (Aira et al. 2010), wheat (Kaci et al. 2005) and sunflower (Alami et al. 2000). Phenotyping of pearl millet lines for rhizospheric soil aggregation potential reveled contrasted lines. for this lines, the soil-aggregation potential was correlated to the diversity and activity of rhizospheric bacterial communities producing exopolysaccharides (Ndour et al. 2017). However, several studies have reported that arbuscular mycorrhizal fungi affect microbial community structure and rhizospheric soil aggregation (Marschner and Baumann 2003).

in addition, the formation and function of mycorrhizal relationships are affected by edaphic conditions such as soil composition, moisture, temperature, pH, Cation Exchange Capacity (CEC), and anthropogenic stressors (Entry et al. 2002). There is limited information of the effect of temperature on the functioning of mycorrhizal symbiosis on millet and its effect on soil aggregation. It was reported that the rise of the temperature can induce an increase the AMFs' internal and external structures (Heinemeyer et al. 2004; Compant et al. 2010; Zhu et al. 2011).

In this study, we investigate the mycorrhization capacity of four millet lines and assess the effects of temperature stress on physiological parameters, mycorrhizal colonization and the mycorrhizal growth response of millet lines. We evaluated also the effect of high temperature treatments on the rhizosphere soil aggregation. We hypothesized that AMF inoculation could alleviate negative effects of temperature stresses on millet lines.

Materials and Methods

Biological Materials

The plant material consisted of four millet lines with contrasting potential for the soil aggregation trait. These include L220 and L3 (low soil aggregation potential) and L132 and L253 (high soil aggregation potential). They are isogenic lines phenotyped based on their soil aggregation potential (Ndour et al. 2017). The seeds were produced by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and obtained from the "Institut de Recherche pour le Développement (IRD)" research center in Senegal throughout the "Laboratoire d'Ecologie Microbienne des Sols et Agro Systèmes Tropicaux (LEMSAT)". The fungal material consisted of AMF strains from the "Laboratoire Commun de Microbiologie" (LCM)'s collection. Two strains including *Rhizophagus aggregatus* and *Funneliformis mosseae were* selected and multiplied separately in the greenhouse on maize (*Zea mays L*) as a host plants (Tian et al. 2013; Ndeko et al. 2019). These were grown 4 months on sterilized sandy soil (autoclaved at 120 °C for 20 min) from Bambey (Table 1). These strains were selected based on their high effectiveness in improving growth, nutrition and drought tolerance on many plant species (Wright et al. 2005; Tian et al. 2013). The inoculum produced was a mixture of infected root fragments, sand, spores and mycelia from the trap cultures (crops) and contained ~40 and 55 spores g^{-1} for *R. aggregatus* and *F. mosseae*, respectively. After production, the inoculum of AMF strains were stored at 4 °C in a cold storage chamber for 20 days before use.

Table 1 Physical and chemical characteristics of the soil used in greenhouse and culture chamber experiments

Soil characteristics	Units	Values
Physical characteristics		
Clay	%	9.2
Fine silt	%	3.4
Coarse silt	%	8
Fine sand	%	59.8
Coarse sand	%	21.2
Chemical characteristics		
pH (H_2O)	–	6.57
pH (KCl)	–	5.16
Total carbon	%	0.4
Total nitrogen	%	0.03
C/N	–	15
Total phosphorus	Mg/kg	78.27
Available phosphorus	Mg/kg	1.05
Calcium	Meq%	3.61
Magnesium	Meq%	1.15
Sodium	Meq%	0.01
Potassium	Meq%	0.06
Cation exchange capacity (CEC)	Meq%	4.43

Experimental Design and Growth Conditions

Two independent experiments were carried out in both the greenhouse and culture chamber to compare the ability of four pearl millet lines to mycorrhizal inoculation and assess the effect of temperature stress on mycorrhization and soil aggregation on pearl millet lines, respectively. The greenhouse experiment was conducted from January to April 2018, while the culture chamber experiment was conducted from April to August 2018 at the "Laboratoire Commun de Microbiologie" (IRD/ISRA/UCAD) located at BelAir, Senegal. The soil used in these experiments was collected from the experimental site of the National Centre for Agricultural Research (CNRA/ISRA) at Bambey region (1442′38.7″N and 1628′47.2″W), located in the "Bassin Arachidier" of Senegal where millet is widely cultivated. The soil was an aerosol type (FAO 2006) whose physical and chemical compositions are presented in Table 1. Physicochemical and microbiological analyses of the soil samples were carried out respectively in the "Laboratoire des moyens analytiques" (LAMA) and in the Common Microbiology Laboratory (IRD/ISRA/UCAD) located in the IRD/ISRA/UCAD research center at Bel-Air, in Dakar, Senegal.

Experiment 1: Response of Four Pearl Millet Lines to Mycorrhizal Inoculation

Experimental Design

This experiment was conducted in greenhouse conditions using a two-factor completely randomized block design. The factors included: (a) mycorrhizal inoculation (*R. aggregatus, F. mosseae* and the control treatment without inoculation) and (b) genotype with 4 millet lines (L3, L220, L132 and L253). The combination of factors gave a total of 12 treatments (Inoculation × Lines). Ten replications (equivalent to 10 plants) were used for each treatment. The 12 treatments were as follows: (1) L3-Non-AMF plants, (2) L3 + *R. aggregatus*, (3) L3 + *F. mosseae*, (4) L220-Non-AMF plants, (5) L220 + *R. aggregatus,* (6) L220 + *F. mosseae,* (7) L132-Non-AMF plants, (8) L132 + *R. aggregatus,* (9) L132 + *F. mosseae*, (10) L253-Non-AMF plants, (11) L253 + *R. aggregatus,* and (12) L253 + *F. mosseae*. The choice of AMF strains was made on the basis of their performance in previous studies. In order to properly measure soil aggregation, plants were grown in special bottomless pots made of two parts that could be easily detached without altering the plant root system. Each pot was filled with 1.5 kg of soil and inoculated before sowing on non-sterilized soil. Five seeds were sown per pot and thinned to one plant 10 days after seedling emergence. Used seeds were disinfected with a sodium hypochlorite solution (8% active chloride, 15 min) and rinsed three times with sterilized (at 121 °C for 15 min) deionized water (for 10 min). In total, the experiment consisted of 10 non-AMF plants, 10 plants inoculated with *R. aggregatus,* and 10 plants inoculated with *F. mosseae* for each millet line. For each AMF strain, 30 g of inoculum were used for AM inoculation in pots, while plants without AM inoculation were supplemented with 30 g of autoclaved (dead) inoculum. The inoculum was placed at ~4 cm deep in contact with seeds. Pots were placed 20 cm apart on the greenhouse bench to prevent contamination. Plants were watered daily as needed at the 80% of the field capacity with distillated water throughout the whole period of the experiment. Plants were grown until physiological maturity before they were harvested.

Data Collection

The above ground (shoot) and underground (root) biomasses, mycorrhizal colonization and soil aggregation were measured at the 60th day after sowing. At harvest, roots were carefully removed from the soil and washed under running water and separated from the aerial parts. The dry weight of above and underground biomasses was determined after drying in an oven at 65 °C for 72 h. In addition, the total biomass including, the above- and below-ground biomasses, was determined using a weighing balance. Some root samples (2 g) were collected to assess the levels of mycorrhizal colonization of millet lines.

The assessment of the mycorrhizal colonization rate of a millet line was performed on root samples taken from inoculated and non-inoculated plants. At harvest, root samples were rinsed with distilled water, taken and preserved in 70% ethanol before staining (Heinemeyer et al. 2004). The collected roots were placed in tubes and stained according to Pierre et al. (2020). The root samples were then placed in a 10% KOH solution (W/V) and incubated in a 90 °C water bath for 1 h. Roots were then soaked in a 0.05% Trypan blue solution and the tubes were further incubated in a water bath at 80 °C for 30 min. Measurement of the AMF root colonization rate was performed using the root intersection microscopy method with a compound stereo microscope as reported by Jerbi et al. (2020). Finally, the response of millet lines to inoculation with different arbuscular mycorrhizal fungus was determined by the calculation of the Mycorrhizal Growth Response (MGR) according to Raya-Hernández et al. (2020). The following formula was used:

$$MGR = \frac{\mathrm{TB(Myc)} - \mathrm{TB(Non\ Myc)}}{\mathrm{TB\ (Myc)}} \times 100$$

With MGR: Mycorrhizal Growth Response, TB (Myc): the total biomass of inoculated plants and TB (Non Myc): the total biomass of uninoculated plants.

Soil Aggregation Measurement

At harvest, the two parts of the pot were detached and the mass of adhering soil to the roots was determined. The plants were attached to an electric agitator (S50, CAT, Staufen, Germany) and shaken at a constant speed (1100 rpm/min) for one minute to separate the mass of non-adhering from adhering soil (see Fig. SM1 in Supplementary Material). The root adhering soils were collected on cups with sterile distilled water and dried at 105 °C for 72 h and then weighed. Soil aggregation was determined by the ratio of the mass of adhering soil (MAS) and the root biomass (MAS/RB).

Experiment 2: Assessment of the Effect of Temperature Stress On Mycorrhization and Soil Aggregation in Millet Lines

Experimental Design

This experiment were conducted using two controlled growth chambers, model E15 with a comp 3244 controller (Conviron, Controlled Environments Ltd., Mani-

toba, Canada), to evaluate the effect of temperature stress and AMF inoculation on millet lines growth, mycorrhizal colonization, MGR and soil aggregation. The experiment was a three-factor completely randomized block design. The factors included: (a) millet lines (L3, L220, L132 and L253), (b) mycorrhizal inoculation (*R. aggregatus, F. mosseae* and control treatment without inoculum) and (c) temperature treatment (high temperature treatment: 37/33 °C and control treatment: 32/28 °C). The combination of factors generated a total of 24 treatments (Lines × Inoculation × Temperature stress) conducted with 10 replications (equivalent to ten plants per treatment).

The millet plants were grown in WM pots of 2.0-litre volume capacity filled with the soil from Bambey (Table 1). Five seeds per pot were sown, followed by thinning to one plant per pot 10 days after sowing (DAS). The conditions within the control chamber were maintained at optimum temperature: 32/28 °C (day/night temperature). The photoperiod was 16 h, and the photosynthetic photon flux density (PPFD) was ~300 µmol m^{-2} s^{-1}. On the other hand, the temperature stress chamber as set at 37/28 °C (day/night temperature) while other parameters were maintained as in the control treatment. The relative humidity (RH) in both chambers was between 40 and 65%. All plants were grown in the control and high temperature chambers for 60 days. In both chambers, pots were randomly moved every week to avoid the environmental effects within the chambers.

Data Collection

All plants per treatment were harvested 60 days after sowing. Growth (plant high, shoot biomass, root biomass, leaf area), physiological (chlorophyll concentration) and mycorrhization (mycorrhizal colonization rate, MC) parameters were measured. The MGR of millet lines and the rhizospheric soil aggregation (Masse of adhering soil/Root biomass, MAS/RB) were also determined. The whole plant was harvested followed by separation of the above-ground part and the root system. Dry weights were recorded after drying the plant parts at 65 °C for 72 h to determine the shoot and root biomasses. Plant height and the leaf area were recorded before harvesting. The leaf area was measured by the "Length-Width" method which considered the number of leaves N and the average of the "Length × width" products of the selected leaves (3 leaves per plant) according to (Persaud et al. 1993). Finally, chlorophyll concentration was measured before harvesting using the SPAD-502Plus chlorophyll meter (Uddling et al. 2007). The root samples were washed in tap water, stored in ethanol (70%) and maintained at 4 °C before measuring the AMF colonization.

Data Treatment and Analysis

The statistical analysis was carried out using R 3.6.1 and Microsoft excel® XLSTAT package (XLSTAT paris, 2017). For the first experiment, plant growth, soil and mycorrhizal parameters (shoot dry weight, root dry weight, mycorrhizal colonization and mycorrhizal growth response) were analyzed by a two-way ANOVA ($p < 0.05$). For the second experiment, physiological, growth, soil and mycorrhizal parameters (root dry weight, shoot dry weight, plant height, leaf area, chlorophyll concentration, mycorrhizal colonization, MGR and soil aggregation) were analyzed by a three-way ANOVA under a randomized complete block design. Differences among the treatments' means were separated with the Turkey HSD test at 5% threshold.

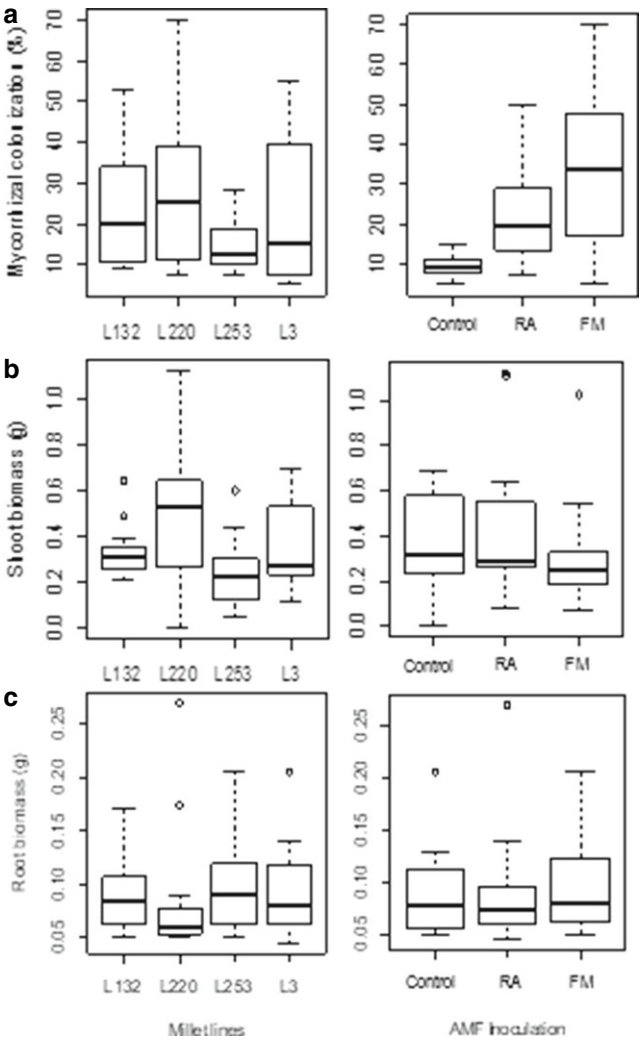

Fig. 1 Arbuscular mycorrhizal fungal colonization (**a**), plant shoot biomass (**b**) and plant root biomass (**c**) of pearl millet lines as affected by AMF strains inoculation (*Rhizophagus aggregatus*, RA, and *Funneliformis mosseae*, FM). Values are means (±SE) of six replicates. Difference between treatments were assessed by the two-way ANOVA ($P < 0.05$)

Table 2 Effects of line, AMF inoculation and their interactions on growth parameters, mycorrhization and soil aggregation under millet crop

Sources of variation	Parameters	SB(g)	RB (g)	Mycorrhizal colonization (%)	MGR (%)	MSA/BR
Lines (L)	Error	0.0491	0.0023	13.95	65.95	10.31
	F	4.185	0.354	2.376	2.19	22.64
	P value	0.0096 **	0.78	0.059	0.047*	$9.9e^{-10}$***
AMF inoculation (AMF)	Error	0.238	0.0022	13.95	68.02	12.83
	F	1.204	0.323	2.948	1.07	1.55
	P value	0.3075	0.725	0.045*	0.35	0.22
L*AM	Error	0.0436	0.0023	13.16	65.99	34.49
	F	1.989	1.456	2.062	1.353	10.75
	P value	0.0856	0.213	0.042*	0.233	$1.3e^{-09}$***

Legend: *SB* shoot biomass, *RB* root biomass, *MGR* mycorrhizal growth responses, *MSA/RB* mass of adhering soil, indicating the soil aggregation, *AMF* arbuscular mycorrhizal fungi

Values are means (±SD) of six replicates. Difference between treatments were assessed by the two-way ANOVA ($P < 0.05$). *, **, *** significant at $p = 0.05$, 0.01 and 0.001, respectively

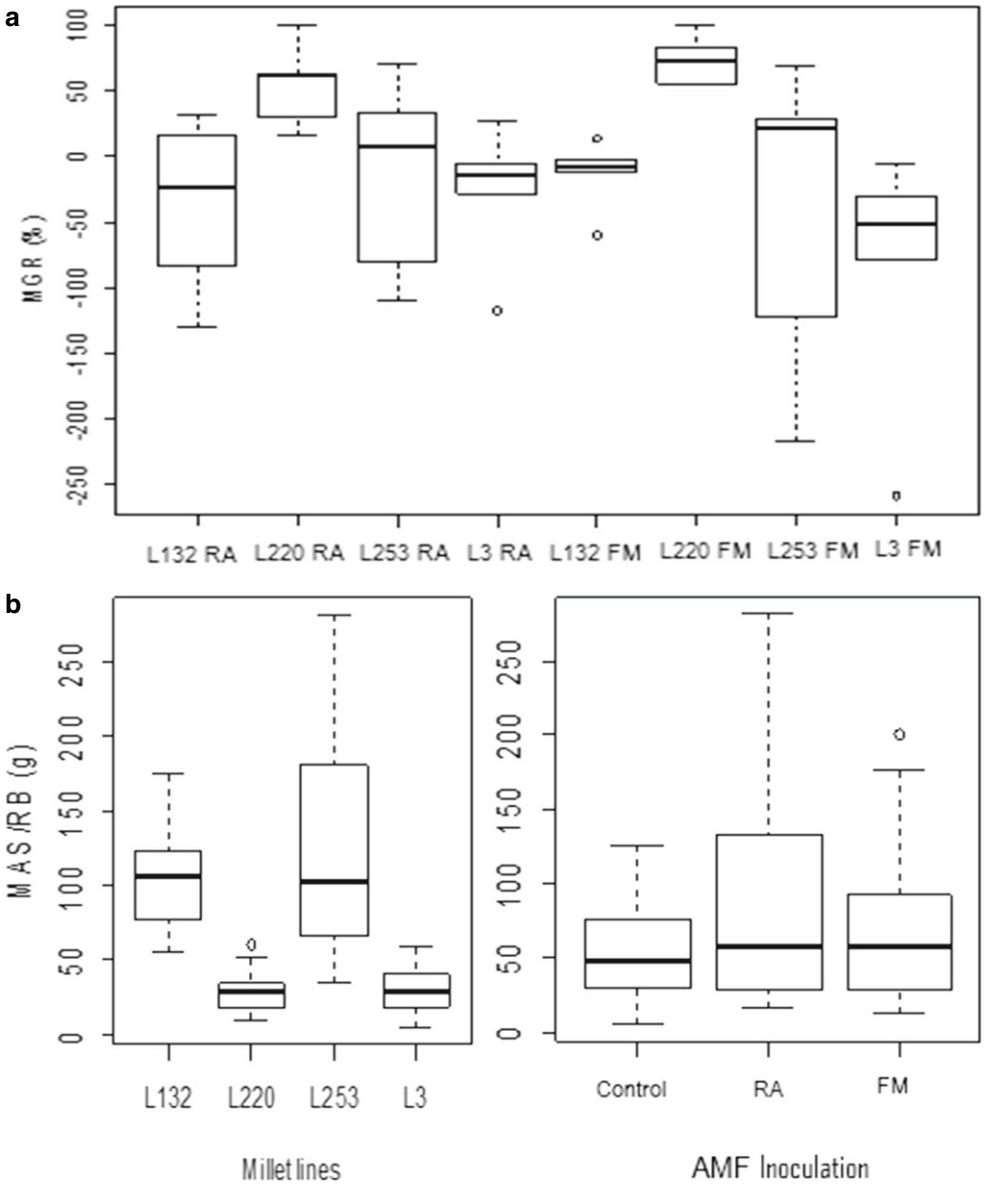

Fig. 2 Mycorrhizal growth response (MGR, (**a**)) and mass of adhering soil/root biomass (soil aggregation, (**b**)) of millet lines as a function of AMF strains inoculation (*Rhizophagus aggregatus*, RA, and *Funneliformis mosseae*, FM) under greenhouse conditions. Values are means (±SE) of six replicates. Difference between treatments were assessed by the two-way ANOVA ($P < 0.05$)

Results

Experiment 1: Mycorrhizal Colonization (MC) and the Mycorrhizal Growth Response (MGR) of Millet Lines Under Greenhouse Conditions

Mycorrhizal Colonization of Millet Lines as Influenced by AMF Strains

Root microscopic examination revealed that mycorrhizal colonization rate was generally low (<50%) and not significantly different ($p=0.059$) among the tested lines (Fig. 1a). AMF significantly affected ($p=0.045$) the mycorrhizal colonization rate of millet lines. *F. mosseae* (32.9%) showed high percentage of root colonization compared to *R. aggregatus* (22.8%) and non-inoculated (Control) (9.8%). The use of non-sterile soil in this study, and non-inoculated plants also was also colonized by AMF due to the presence of some local soil-native AM species.

Growth and Physiological Traits of Millet Lines Under Greenhouse Conditions

There was a significant difference in the shoot biomass ($p=0.005$). However, the root biomass was not affected by lines L220 accumulated more shoot biomass than other lines. There were no significant effects (Table 2) of AMF inoculation on the shoot and root biomasses (shoot and root dry weight). The interaction between the tested lines and the AMF inoculation was not significant for the shoot and root dry weights (Fig. 2). This result suggest that the AMF colonization rate was an indicator of the activity of the mycorrhizae in pearl millet lines.

Mycorrhizal Responsiveness of Millet Lines Under Greenhouse Conditions

The pearl millet lines responded differently to inoculation with AMF strains. Shoot growth responsiveness differed among lines when the plant roots are colonized by AMF. Overall, the mycorrhizal growth response (MGR %) of millet lines ranged from +57% to –84% (Fig. 3). The results showed a significant difference (P=0.003) in the mycorrhizal growth response among the millet lines. L220 and L253 had highest and positive MGR values when colonized by *R. aggregatus* (+57%) and *F. mosseae* (47.4%). L220 recorded highest MGR response values compared to other genotypes (Table 2).

Effects of AMF Inoculation On Rhizospheric Soil Aggregation (MAS/RB) of Millet Lines

Soil aggregation varied widely among millet lines ($p<0.0001$). L132 and L253 had high than L3 and L220 (Fig. 4). In L253, control plants showed low MAS/RB values compared to plants inoculated with *R. aggregatus* and *F. mosseae*, which showed a positive effect of inoculation on soil aggregation.

Experiment 2: Effect of Temperature Stress On Mycorrhizal Growth Response of Pearl Millet Lines

Effect of Temperature Stress and AMF Inoculation On Growth and Physiological Traits of Pearl Millet Lines

Pearl millet plant height decreased by ~12% under the high-temperature treatment ($p<0.001$) and varied significantly among lines ($p<0.001$) (Table 3). L3, L220 and L253 showed high plant heights in both high (37/32 °C) and normal temperature (32/28 °C). Leaf area increased significantly in the high-temperature treatment but not different among lines. Chlorophyll concentration was reduced significantly ($p<0.001$) with the high-temperature and among lines. L3 exhibited highest chlorophyll concentration while L253 and L132 had lowest levels. Root biomass (root dry weight) decreased by 39.1% (L132), 27% (L220), 37.8% (L3), and 58.6% (L253) under high-temperature treatment. A significant interaction was observed between lines and treatments for root biomass ($p=0.044$). L253 had accumulated highest root biomass under non-stress conditions. The rising of temperature decreased root biomasses in L3, L132 and L253. For L220, however, no significant difference between the control (32/28 °C) and high-temperature treatments (37/32 °C) was observed (Table 3). Shoot biomass (shoot dry weight) also decreased significantly under temperature stress conditions ($p=0.046$), but no differences were founded between lines (Table 3). The decline in shoot dry weight was more pronounced on L253 (34.9%) and L132 (32.7%) under temperature stress conditions than on L3 (11.2) and L220 (20.3%).

The effect of AMF inoculation on plant height, leaf area, chlorophyll concentration, shoot biomass and root biomass varied with millet lines under temperature treatments (Table 3). For all lines, plant height was unaffected by either of AM inoculation when plant was exposed to optimal (control) temperature. At high temperature treatment, lines showed increased plant height with AMF inoculation, but there were no significant differences between *F. mosseae* and *R. aggregatus*. On L3, L132 and L253, leaf area significantly increased with AMF inoculation under high temperature treatment only. On L220, AMF inoculation affected leaf area in both high and control treatments. Plants in-

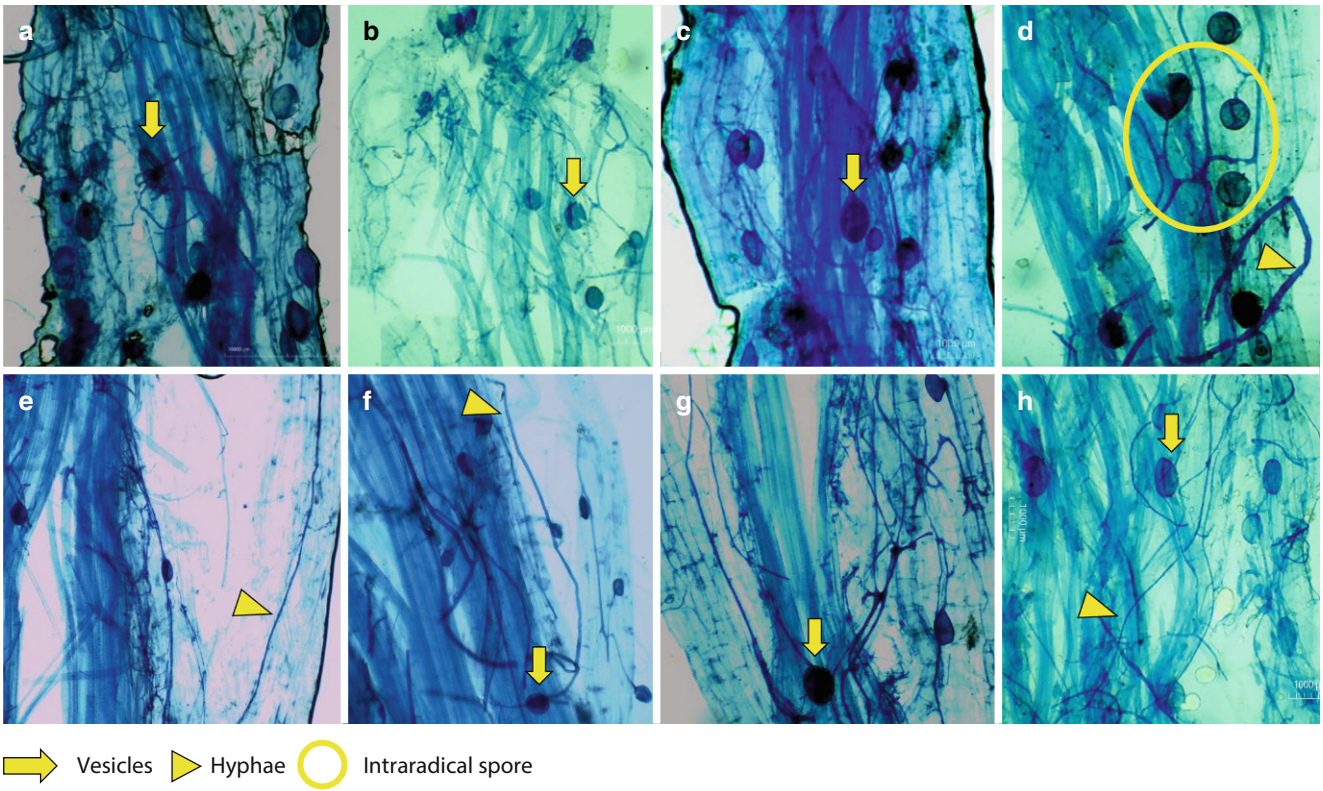

Fig. 3 Mycorrhizal root colonization of pearl millet lines by *Funneliformis mosseae* (**a**, **b**, **c**, **e**, **f**, **g**) and *Rhizophagus aggregatus* (**d**, **h**) under control and high temperature treatments in culture chamber. **a** L253 at 32–28 °C (day-night temperature), **b** L220 at 32–28 °C, **c** L132 at 32–28 °C, **d** L3 at 32–28 °C, **e** L253 at 37–32 °C, **f** L220 at 37–32 °C, **g** L132 at 37–32 °C, **h** L3 at 37–32 °C. *Arrow*: vesicles; *triangle*: hyphae; *circle*: intraradical spore

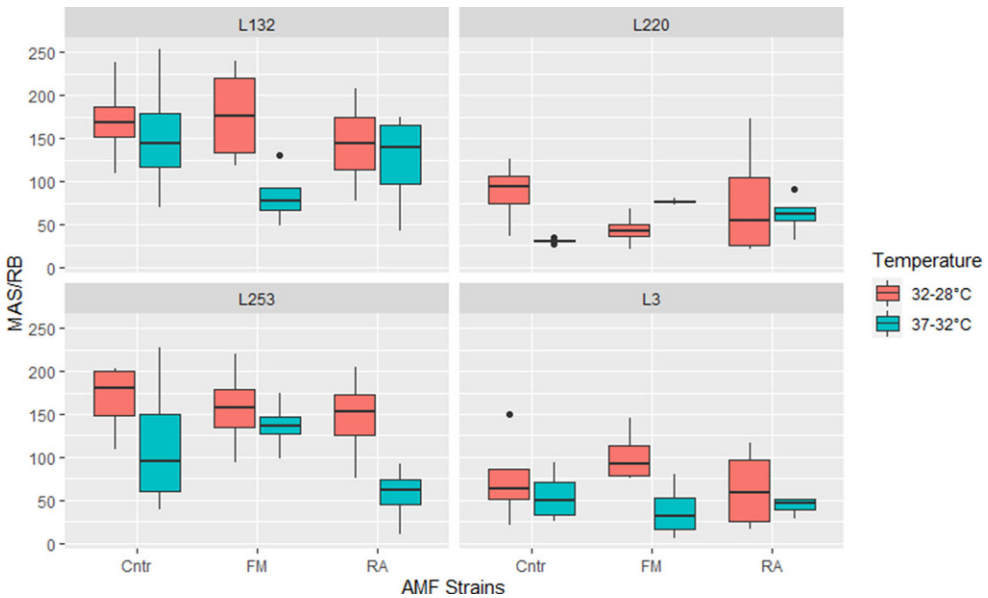

Fig. 4 Soil aggregation (MAS/RB) of pearl millet lines as affected by AMF inoculation and temperature treatments. *RA* Rhizophagus aggregatus, *FM* Funneliformis mosseae, *MAS/RB* mass of adhering soil/root biomass

Table 3 Effects of genotypes and temperature treatment interactions on growth and physiological parameters of millet lines

Temperature stress	Pearl millet lines	Mycorrhizal inoculation	Plant height (cm)	Leaf area (cm^2)	Chlorophyll concentration (SPAD values)	Shoot biomass (g)	Root biomass (g)
32–28 °C	L132	Control	38.25ef	116.26bcd	25.93gh	0.65bcd	0.10bcd
	L132	*R. aggregatus*	33.75f	98.04def	26.58ef	0.73abc	0.12bcd
	L132	*F. mosseae*	39.75ef	113.63bcd	27.35 cd	0.67bcd	0.16bc
37–32 °C	L132	Control	41.37de	95.68def	25.0gh	0.32g	0.068 fg
	L132	*R. aggregatus*	41.6de	106.97cde	26.25ef	0.51ef	0.09def
	L132	*F. mosseae*	47.52bcd	134.59ab	26.9ef	0.55ef	0.14bcd
32–28 °C	L220	Control	42.25de	59.97g	27.13def	0.58e	0.13bcde
	L220	*R. aggregatus*	45.75cde	70.01 fg	29.72abc	0.67bcd	0.13bcde
	L220	*F. mosseae*	47.75bcd	114.87bcd	29.3abc	0.78ab	0.11bcde
37–32 °C	L220	Control	44.7bc	42.47h	25.44gh	0.42 fg	0.06g
	L220	*R. aggregatus*	50.2ab	123.38ab	29.53abc	0.58cde	0.12bcde
	L220	*F. mosseae*	52.55ab	99.96def	28.7bcd	0.61cde	0.09def
32–28 °C	L253	Control	39.75ef	76.23efg	25.15gh	0.61cde	0.16b
	L253	*R. aggregatus*	39.5ef	74.16efg	25.75gh	0.83ab	0.24a
	L253	*F. mosseae*	46.0bcd	113.26 cd	29.43abc	0.89a	0.1cde
37–32 °C	L253	Control	41.85def	69.33gh	23.05i	0.47ef	0.064g
	L253	*R. aggregatus*	52.12ab	159.33a	24.05i	0.48ef	0.066g
	L253	*F. mosseae*	51.26ab	142.58ab	24.38hi	0.60cde	0.07 fg
32–28 °C	L3	Control	47.37bcd	93.83def	28.08bcd	0.60bcd	0.11bcd
	L3	*R. aggregatus*	42.88bcd	79.85efg	32.4a	0.65bcd	0.12bcd
	L3	*F. mosseae*	47.5bcd	79.39efg	31.3ab	0.63bcd	0.14bcd
37–32 °C	L3	Control	45.4bc	87.5 fg	27.6cde	0.44f	0.066g
	L3	*R. aggregatus*	54.18a	109.47 cd	28.18bcd	0.53def	0.091de
	L3	*F. mosseae*	52.65ab	130.3ab	29.15abc	0.65bcd	0.085de
P value							
Lines (L)			<0.0001***	0.06*	<0.0001***	0.27	0.47
Inoculation (I)			0.056	0.01**	0.016**	0.046*	0.04*
Temperature stress (HS)			<0.0001***	<0.0001***	<0.0001***	0.1	<0.0001***
*L*HS*I*			0.62	0.31	0.41	0.09	0.02*

, **, * significant at p = 0.05, 0.01 and 0.001, respectively. Means followed by different letters are significantly different at 5% p-value threshold of the Tukey's HSD test.*

oculated with *F. mosseae* showed increased leaf area than *R. aggregatus* and uninoculated plants. Chlorophyll concentration differed between AM-inoculated and non-inoculated plants in L220 under both high and control temperature treatments. Chlorophyll concentration increased with AM inoculation but the statistical analysis displayed no significant differences between *R. aggregatus* and *F. mosseae.* On L3 and L253, chlorophyll concentration significantly increased with AMF inoculation only under high temperature treatment. On L132, AMF inoculation did not affect the chlorophyll concentration in both high and control temperature treatments. Shoot biomass did not vary among millet lines but significantly increased with AM inoculation ($p = 0.049$) in L220 and L253 regardless of the thermal regime. On the other hand, AMF applications did not increase significantly the root and shoot dry weights under control treatment (non-stress conditions) for L3 and L132 lines. However, when exposed to temperature stress, plants inoculated by *R. aggregatus* and *F. mosseae* showed a significant rise in shoot biomass as compared to uninoculated plants. AMF inoculation affected significantly the root biomass of millet lines ($p = 0.04$). At high temperature treatment, only L220, L132 and L3 had increased root biomass when inoculated with AMF strains. However, for L253, inoculation only had a significant effect under non-stress conditions.

Effect of Temperature Stress On Mycorrhizal Colonization Rate and Mycorrhizal Growth Response (MGR) and Soil Aggregation

This study showed a significant difference ($p < 0.001$) in the percentage of root colonization between control and high-temperature treatments. Mycorrhizal colonization signifi-

Table 4 Mycorrhizal colonization and soil aggregation as affected by millet genotypes and different temperature treatments

Temperature stress	Millet lines	Mycorrhizal inoculation	Mycorrhizal colonization (%)	MGR (%)	MAS/RB
32–28 °C	L132	Control	25.03hij	–	170.9a
	L132	*R. aggregatus*	64.79bc	–23.345d	143.68abc
	L132	*F. mosseae*	67.4ab	–13.66cd	177.6a
37–32 °C	L132	Control	13.5l	–	101.68bcde
	L132	*R. aggregatus*	25.8hij	6.27bcd	85.76def
	L132	*F. mosseae*	31.6ghi	20.8abc	82.8def
32–28 °C	L220	Control	20.4jkl	–	56.6fgh
	L220	*R. aggregatus*	60.75bcd	27.29abc	75.86efg
	L220	*F. mosseae*	80.75a	36.19ab	43.48ghi
37–32 °C	L220	Control	10.54l	–	28.19i
	L220	*R. aggregatus*	42.67efg	4.63bcd	42.2gh
	L220	*F. mosseae*	61.75bc	59.76a	45.06gh
32–28 °C	L253	Control	15.2jkl	–	97.24cde
	L253	*R. aggregatus*	55.25bcd	–68.13e	146.26abc
	L253	*F. mosseae*	70.43ab	23.84abc	156.96ab
37–32 °C	L253	Control	9.8kl	–	70.49efgh
	L253	*R. aggregatus*	25.83hij	31.82ab	51.41fgh
	L253	*F. mosseae*	18.33ijk	–4.23bcd	111.89bcde
32–28 °C	L3	Control	10.19jkl	–	67.05efgh
	L3	*R. aggregatus*	50.58cde	–13.9e	77.66defg
	L3	*F. mosseae*	45.5def	1.71bcd	101.1cdef
37–32 °C	L3	Control	11.23kl	–	44.34fgh
	L3	*R. aggregatus*	20.42hij	–5.1bcd	42.64ghi
	L3	*F. mosseae*	24.58hij	5.968bcd	36.032hi
P value					
Lines (L)			<0.0001***	0.016*	<0.0001***
Inoculation (I)			<0.0001***	0.015*	0.47
Temperature stress (HS)			<0.0001***	0.045*	<0.0001***
*L*HS*I*			0.008**	0.018*	0.23

, **, * significant at p = 0.05, 0.01 and 0.001, respectively. Means followed by different letters are significantly different at 5% p-value threshold of the Tukey's HSD test.*

cantly decreased in high-temperature treatment (Fig. 3 and Table 4). A significant difference ($p = 0.003$) in mycorrhizal colonization was also observed between the millet lines. L220 and L132 (47.7% and 44.2%, respectively) showed more mycorrhizal colonization as compared to other genotypes under control and high-temperature treatments. No significant interaction between genotype and heat treatment was detected. The mycorrhizal growth response significantly ($p = 0.005$) increased with high-temperature treatment and significantly differed ($p = 0.02$) among millet genotypes. Results showed that the greatest and most positive mycorrhizal growth response was from L220 and L132 compared to other genotypes in high-temperature treatment (Table 4). Negative MGR values were observed on L132, L3, and L253 in the control treatment (32/28 °C). In general, we observed that MGR was significantly better under temperature stress than in the control treatment and varied among lines. AMF mycorrhizal inoculation significantly affected root colonization and the mycorrhizal growth response. We also observed significant interaction between lines, temperature stress and mycorrhizal inoculation ($p = 0.018$). Regardless of the thermal regime applied, AMF inoculation significantly improved the mycorrhization rate of all lines. High mycorrhizal colonization and mycorrhizal response were obtained by using *F. mosseae.*

Effect of Temperature Stress On the Soil Aggregation (MAS/RB) in the Rhizosphere of Pearl Millet Lines

Results from this study (Table 4) showed that the soil aggregation was reduced significantly ($p < 0.001$) under high-temperature treatment and was also significantly different ($p < 0.001$) among genotypes. L132 and L253 recorded the highest MAS/RB ratio in both control and high temperature treatments while L3 and L220 had lowest MAS/RB. The inoculation did not significantly influence the MAS/RB ratio

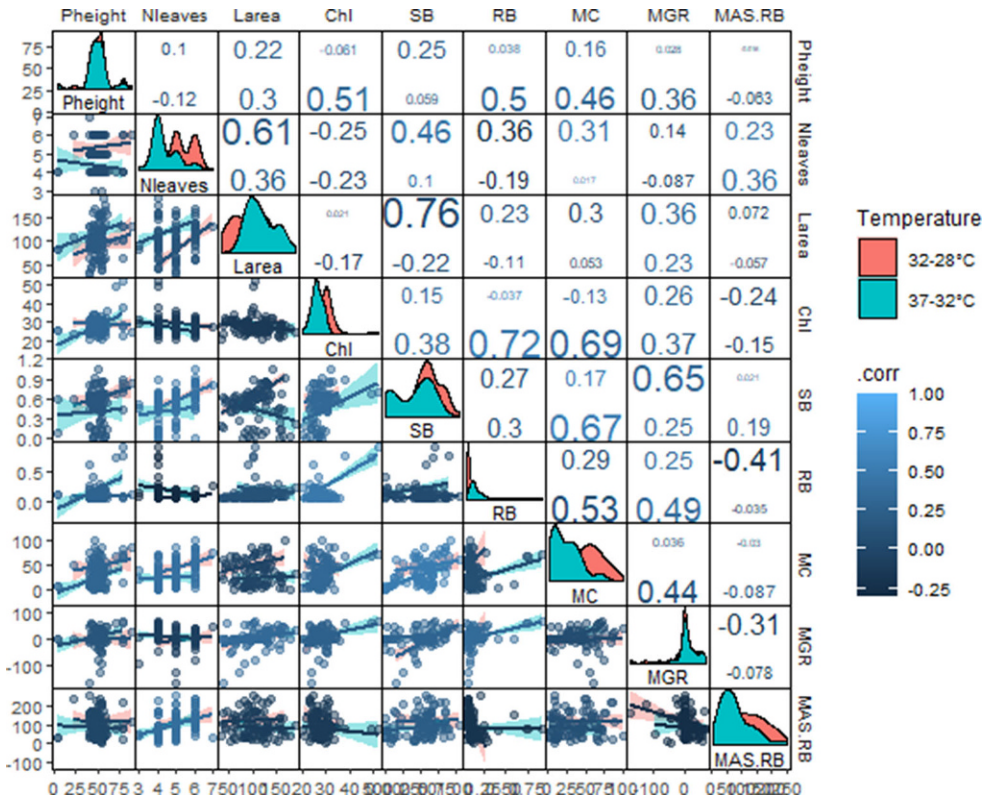

Fig. 5 Pearson's correlation matrix between growth, physiological parameters, soil aggregation and AMF root colonization. Plant height (Pheight), number of leaves (Nleaves), leaf area (Larea), hhlorophyll concentration (Chl), shoot biomass (SB), root biomass (RB), mycorrhizal colonization rate (MC), mycorrhizal growth response (MGR) and mass of adhering soil/root biomass (MAS/RB)

regardless the heat treatment. There were no significant effects of the interaction between AMF inoculation and temperature treatments for the soil aggregation. The differences observed in soil aggregation among lines could be explained by line-specific traits for this variable (Table 4). However, the inoculation seemed to positively influence soil aggregation regardless of the temperature treatment. For L220, soil aggregation increased in high-temperature treatment when root was colonized by *F. mosseae* (Fig. 4). Whereas, for L132, a depressive effect of inoculation on soil aggregation was observed and we had no visible effect on L3.

The Pearson's correlation analysis was used to assess the relationship between AMF colonization and all growth and physiological parameters (Fig. 5). Under the control treatment, the results indicate that no significant correlation was observed between mycorrhizal colonization and the growth parameters of the millet lines. In contrast, under the temperature stress treatment, mycorrhizal colonization of millet lines was highly and positively correlated with plant height (r = 0.46), chlorophyll concentration (r = 0.69), shoot biomass (r = 0.67), root biomass (r = 0.53) and MGR (0.44). There were no significant relationships between number of leaves, leaf area, MAS/RB (soil aggregation) and AMF colonization.

Discussion

Arbuscular Mycorrhizal Fungal Colonization of Pearl Millet Lines

The symbiotic relationship between plants and AMF is the oldest one existing in terrestrial ecosystems and involved in enhancing plant growth, mineral nutrition and stress tolerances (Fahey et al. 2016; Begum et al. 2019). Its role in enhancing stress tolerance was reported by other studies but they did not consider the effect of plant genotypes. This study highlighted differences in responses of millet lines to inoculation with two AMF strains and the significant effect of temperature stress on mycorrhization, plant growth and soil aggregation. The result reveals that, only L220 and L253 responded positively to all inoculated AMF strains. This response would be the result of an improvement in the nutritional status of the plants ensured by developing a network of extraradicial hyphae of the fungus and by the extension of the soil volume explored by the roots (Benjelloun et al. 2014). Early reports showed that cultivars react differently to an AMF strain (Seifi et al. 2014). Similar effects on mycorrhization have been observed in fonio (Ndoye et al. 2016), cowpea (Diop et al. 2013), tamarind (Bourou et al. 2011), and maize (Miller and Yastrow 2000). In date palms, Zougari-Elwedi et al. (2012) observed an increase in biomass (+45%) and in the

levels of phosphorus, nitrogen, potassium, copper and zinc in inoculated young plants. This is in line with Plenchette et al. (1999) who concluded that millet have a low mycorrhizal dependency although growth stimuli are observed (El Mrabet et al. 2017). Higher rates of mycorrhizal colonization have been observed in other cereals in controlled conditions (Nouaim and Chaussod 1996). This suggests that there is a high degree of variability between different millet lines in their response to mycorrhizal inoculation. Several factors can affect mycorrhizal colonization and the response of plants to mycorrhizal inoculation. According to Sensoy et al. (2007), the genotype of the host plant is an important determinant of the response to mycorrhizal inoculation.

Arbuscular Mycorrhizal Fungal Colonization of Pearl Millet Lines in Relation to the Soil Aggregation

Soil aggregation is an important aspect of ecosystem functioning in terrestrial ecosystems. Arbuscular mycorrhizal fungi (AMF) play a key role in soil aggregate formation and stabilization (Rillig and Mummey 2006). In the present study we find that millet lines maintained their soil aggregation potential regardless of whether or not mycorrhizal fungi are applied. Lines 132 and 253 had high MAS/RB values while lines 3 and 220 had low values. Inoculation with AMF strains did not significantly influence the MAS/RB ratio of millet lines. The contribution of AMFs to soil aggregation and aggregate stabilization depends largely on the textural characteristics of the soil under consideration (Miller and Yastrow 2000). Inoculation with an AMF strain has different effects on aggregation depending on the soil type. Under these conditions, sandy soil and loamy soils have very poor aggregation compared to organic soil (Bethlenfalvay and Barea 2009). In our context, the characteristics of the soil and plant genotypes used could have an impact on mycorrhiza formation and on the production of glomalin, a glycoprotein produced by the AMF and involved in the soil aggregation process (Wright et al., 2007). In fact, mycorrhizal establishment produce an increase in glomalin concentration and there is a positive correlation between Glomalin concentration, soil aggregation and AMF root colonization (Bedini et al. 2009). Early reports showed soil that structure determined the level of soil aggregation. The same results in pea, inoculation of pea plants with *Funneliformis mosseae* increased the level of soil aggregation more significantly in a silty soil (400%) than in a clay soil (50%). On the other hand, the root systems of plants and their rhizospheres have a great influence on soil aggregation. The mechanisms involved include root penetration, modification of the soil water regime, root exudation, decomposition of dead roots and root entanglement, which vary widely between plant genotypes (Bronick and Lal 2005). The influence of mycorrhizal fungi on soil aggregation is, therefore, only possible when carbohydrate production is not limited by other external factors, which would also limit the proper functioning of mycorrhizal symbiosis (Singh et al. 2014).

Effect of Temperature Stress and Arbuscular Mycorrhizal Fungal Inoculation On Millet Line Development and Soil Aggregation

In response to temperature stress, results showed that the mycorrhizal colonization of millet genotypes significantly decreased in high temperature treatment than in control treatment. The increase in temperature induced a reduction in mycorrhizal colonization in all millet lines. Extreme environmental conditions can negatively affect some beneficial microorganisms such as Arbuscular Mycorrhizal Fungi (Jerbi et al., 2020). Indeed, the effect of temperature stress on mycorrhization depends on the plant species and inoculated AMF strains (Heinemeyer and Fitter 2004). The effects of increased temperature on beneficial plant-associated microorganisms is more variable, positive, neutral, and negative effects can be observed, but varies according to the study system and the temperature range investigated. Temperature can also significantly alter the hyphal network structure of AMF and induce a reduction in vesicle and hyphae (Compant et al. 2010). Under high temperature treatment, the reduction of host plant's photosynthetic capacity resulting in a low allocation of carbon to the fungus, could thus reduce the AMF colonization (Heinemeyer et al. 2006). These results disagree with those of Zhu et al. (2011) on maize grown at 25, 35, and 40 °C. Indeed, the temperature rise did not significantly reduce the mycorrhizal colonization rate of maize plants inoculated with *Glomus etunicatum*. However, Gavito et al. (2005) showed that a temperature increase of up to 30 °C can promote the development of AMF. In addition, Lekberg and Koide (2008) observed a reduction in the mycorrhization rate in sorghum plants inoculated with *Glomus etunicatum* and *Funneliformis mosseae under* the same conditions.

No significant effect of AMF inoculation on growth and physiological parameters was found under non-stress conditions (32/28 °C), but when exposed to temperature stress, plants inoculated by *F. mosseae* and *R. aggregatus* showed a significant rise in shoot dry weight, root dry weight, chlorophyll concentration, mycorrhizal colonization, mycorrhizal growth response and the soil aggregation. Early reports showed that AM colonization could enhance plant biomass and mineral accumulation under temperature stress conditions. Mycorrhizal colonization could enhance photosynthetic activity and plant biomass under temperature stress conditions (Heinemeyer et al. 2006). Fahey et al. (2016) found that AMF inoculation increased root, and shoot biomass and respiration rate under temperature stress, whereas the AMF effect varied among species. Our results

confirm a previous study concerning the effects of different AM fungal taxa on plant growth under environmental stress (Duc et al. 2018).

Our results also showed the significant influence of temperature stress on the rhizospheric soil aggregation of millet lines. An increase in temperature significantly decreased the MAS/BR ratio in millet genotypes. In the present study, we observed that chlorophyll concentration decreased significantly under temperature stress in uninoculated treatment. Root and shoot biomass also decreased in the same conditions, implying low photosynthetic activity and reduced carbon allocation to the root zone. But the reduced carbon allocation could significantly impact root exudation and soil microbial activity, which is actively involved in the soil aggregation process (Duc et al. 2018). These authors showed that AM symbiosis considerably elevated chlorophyll concentration in tomato plants, particularly when inoculated with *Septoglomus constrictum*. Though, in contrast with our result, they have more effect under combined drought and temperature stress. Indeed, it is recognized that climatic parameters such as temperature and precipitation have a strong direct or indirect influence on the soil aggregation (Bronick and Lal 2005). Their influence on soil organic carbon determines the level of soil aggregation (Albrecht et al. 1998). In particular, temperature affects soil aggregation by influencing the nature of microbial populations involved in the decomposition of soil organic matter and by determining the rate of decomposition (Mataix-Solera et al. 2011). The maintenance of the level of soil aggregation in L132 and L220 under temperature stress conditions (37/32 °C) could be related to their ability to associate with AMF under these conditions. Bunn et al. (2009) obtained similar results on two thermopylic plants (*Chanthelium lanuginosum* and *Eragrostis scabra*). They suggested that the mycorrhization improves the growth of thermophilic plants under temperature stress conditions. In addition, Six et al. (2004) established a link between the root system development and soil aggregation. Plant roots and their rhizosphere have a great influence on aggregation through rhizodeposition, decomposition of dead roots and root entanglement. The results of this work suggest that mycorrhization could allow millet genotypes to maintain and improve the soil aggregation level under heat-stress conditions.

Conclusion

The present study investigated the influence of temperature stress and AMF application on mycorrhizal colonization and rhizospheric soil aggregation of millet lines. Results showed that root colonization rate with AMF was low and not different among millet lines. AMF inoculation significantly increased root colonization; *Funneliformis mosseae* showed the highest percentage of root colonization. Millet genotypes responded differently to inoculation with *R. aggregatus* and *F. mosseae*. However, the AMF inoculation did not significantly effect on the rhizospheric soil aggregation of the lines (MAS/RB). As observed in this study, temperature stress significantly affected all the growth and physiological parameters, and had significantly reduced the mycorrhizal colonization rate and the rhizospheric soil aggregation. AMF inoculation had no effect on plant growth under non-stress conditions, however under high temperature treatment; AMF influenced significantly plant growth, mycorrhizal colonization and the mycorrhizal growth response of millet lines. This study showed that the effect of AMF colonization on millet development differs among millet lines. L132 and L220 maintained their soil aggregation level in control and *R. aggregatus* and *F. mosseae* treatments, respectively, because of their mycorrhizal colonization rate and a positive mycorrhizal growth response under high-temperature treatment compared to other lines.

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Conflict of interest A.B. Ndeko, H. Founoune-Mboup, A. Kane and L. Cournac declare that they have no competing interests.

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