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ORIGINAL PAPERS

Mycorrhizal fungi increase plant nutrient uptake, aggregate stability and microbial biomass in the clay soil

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Abstract
Arbuscular mycorrhizal fungi (AMF) are beneficial soil organisms that can form symbiotic associations with the host plant roots. Mycorrhizal symbiosis between plant root and fungi can influence plant diversity and ecosystem productivity. However, the impacts of AMF frequently documented in the loamy to sandy soil, whereas it has no precise mechanism of influencing plant productivity, macronutrient uptake, and aggregation in a clay soil. A pot experiment was carried out to investigate the impact of AMF on plant growth, nutrient uptake and soil aggregation in a clay soil of Bangladesh. Okra (*Abelmoschus esculentus* L.) was cultivated over 105 days with AMF and without AMF (NAMF) with 5 replications. Plant productivity, nutrient uptake, soil organic carbon (SOC), microbial biomass carbon (MBC), aggregate stability (MWD), and glomalin-related soil protein (GRSP) were measured after 105 days. Results showed that the plant productivity and nutrient availability in soil and their subsequent uptake in AMF were significantly higher compared to the NAMF treatment ($p < 0.01$). We observed 17% increase in aggregate stability (measured as mean weight diameter) and 28% increase in organic carbon in AMF inoculated soil compared to NAMF. The microbial biomass carbon and GRSP were significantly higher in the AMF than NAMF treatment ($p < 0.01$). The findings highlight that AMF introduction can be a promising tool for improving plant production and soil condition in the clay soil instead of conventional farming system.

Keywords Plant productivity · Aggregate · Soil organic carbon · Nutrients · GRSP

1 Introduction

Arbuscular mycorrhizal fungi are symbiotic soil microbes, capable of forming a mutualistic association with a diverse range of plant roots (Corcoz et al. 2021; Manga et al. 2022). More than 80% of the terrestrial plants species can for symbiotic association with mycorrhiza (Ma et al. 2022) including agricultural crops (Diagne et al. 2020). The obligatory symbiosis between AMF and plant root can provide varieties of benefits to the host plants and soil such as nutrient uptake, disease control, salinity stress alleviation, drought tolerance, heavy metal pollution prevention, water retention, soil aggregation and soil carbon stabilization (Augé et al. 2001; Ingraffia et al. 2019; Parihar et al. 2020; Chen et al. 2020; Jabborova et al. 2021; Riaz et al. 2021; Topalovic and Vestergård 2021; Agnihotri et al. 2022; Ma et al. 2022; Weng et al. 2022; Pauwels et al. 2023).

The species richness and community composition of mycorrhizal fungi vary across the soils and decrease with increasing soil salinity (Parvin et al. 2019). The mycorrhizal colonization with different plant species varies with soil properties (Halder et al. 2015a, b, e, 2016a, b; Halder et al. 2015c). Halder et al. (2015b) reported that the macro and micro-nutrients uptake in *Ipomea aquatica* were increased under sandy soil due to the influence of AMF. Mollaa and

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Solaiman (2009) found that the commonly cultivated leguminous crops exhibit a high degree of mycorrhizal colonization, ranging from 20 to 76% in tropical clay soil. The genus *Glomus* was the frequently identified, while *Sclerocystis* was the least identified genus of mycorrhiza in the coastal clay soils (Mollaa and Solaiman 2009; Dhar and Mridha 2006). Moreover, the clay soil struggles to maintain resilience in terms of soil quality and plant productivity due to nutrient deficiencies, particularly P, salinity stress, and excessive use of chemical fertilizer (Menge 1983; Khanom and Salehin 2012). Menge (1983) found that P availability in the soils of Bangladesh is lower (having greater immobile P), and lacks other macronutrients. In addition, clay soils of Bangladesh are confronting substantial challenges, notably soil salinity issues at the root zone due to saltwater intrusion because of climate change. Furthermore, intensive application of chemical fertilizers and conventional tillage practices in this region led to a reduced percentage of SOC (Rabbi et al. 2008b; Khanom and Salehin 2012; Haque et al. 2019; Ashrafuzzaman et al. 2022). Nevertheless, AMF colonization can mitigate salt stress to host plant by improving plant nutrient uptake, facilitating ion balance in the soil, and promoting increased rate of photosynthesis (Hajiboland et al. 2009; Aliasgharzadeh et al. 2001; Sheng et al. 2008). Hence, integrating AMF with modern farming can improve soil and plant productivity by enhancing soil aggregation through production of extensive hyphal network and GRSP (Tisdall 1991; Rillig et al. 2010; Alizadeh et al. 2021; Klinsukon et al. 2021). Many previous studies have explored the influence of AMF on plant shoot, root biomass, soil enzymatic activities, SOC, and aggregation in the loamy to sandy texture soil (Schreiner et al. 1997; Andrade et al. 1998; Caravaca et al. 2002; Kohler et al. 2006, 2009; Siddiky et al. 2012; Leifheit et al. 2014; Tran et al. 2021). For example, Caravaca et al. (2002) found that AMF application enhanced the aggregate stability, water soluble organic carbon, and enzymatic activities under *Olea europaea* in the silty loam soil under field condition. Kohler et al. (2009) observed that the shoot, root biomass and soil aggregation were increased upon AMF application under *Lactuca sativa* in the 9-week controlled environment under loam texture soil. Siddiky et al. (2012) found that AMF impacts positively on soil aggregate stability in the sandy soil under a pot experiment growing with *Plantago lanceolata*. However, the impacts of AMF on plant productivity, nutrient acquisition, and soil aggregation in the clay soils remain largely elusive.

The positive impacts of AMF inoculation on plant growth and various physiological aspects have been documented in number of plant species, such as sorghum (Chandra et al. 2022), cherry tomato (Wang et al. 2022), cowpea (Abeer et al. 2015) and okra (Jabborova et al. 2021). AMF symbiosis stimulates plant growth and productivity in host plants by improving the mobilization and absorption of water and mineral nutrients from soil (Li et al. 2022). The dense hyphal network of AMF can expand beyond the nutrient-depleted zones and penetrate smaller soil pores, enabling access to a larger volume of soil for enhanced nutrient assimilation (Rillig 2004; Schaefer et al. 2021). It also improves the availability and translocation of nutrients, especially the elements whose ionic forms have low concentration and limited mobility such as P (Begum et al. 2019; Corcoz et al. 2021). Additionally, the hyphal networks are also capable of absorbing N, K, S and other crucial plant micronutrients, including Ca, Mg, Zn, Cu, B, and Mo (Smith and Read 2010; Fall et al. 2022).

Okra (*Abelmoschus esculentus* L.) is contributing to sustainable food security, widely cultivated and highly consumed vegetables not only in Asia but also in Bangladesh. In Bangladesh, it is considered as a nutritious food for its rich fiber, folate, and vitamin C content, making it a popular healthy choice (Okon 2014). In this study, okra was grown in a nutrient-depleted clay soil of the southwestern Bangladesh with or without AMF incorporation over 3.5 months. We hypothesized that AMF may increase plant growth and productivity by enhancing soil aggregation in the clay soil. The specific objectives were to determine the influence of AMF on (i) Okra productivity and nutrient uptake, (ii) the changes in soil nutrient availability and microbial biomass carbon, and (iii) the stability of soil aggregates.

2 Materials and methods

2.1 Soil

A pot experiment was conducted at the research field of Khulna University, Bangladesh (22°48’ N, 89°32’ E). The average annual temperature and rainfall of the experimental site were 32 °C and 1290 mm, respectively. The initial basic soil properties are presented in Table 1. The soil used in the current investigation was collected from a rice field from 0 to 15 cm depth, which was classified as Typic Haplaquepts (Huq and Shoaib 2013). The soil was air dried and the larger aggregates were broken into smaller sizes with a wooden hammer. The unwanted debris, leaves, weeds, roots, and stones were removed. The soil was passed through 2- mm sieves for the experiment. The sieved soil was sterilized at 121 °C for 30 min through moist heat by autoclaving (Bedini et al. 2009). After autoclaving, initial soil physico-chemical properties were determined.

Table 1 Initial soil properties prior to the pot experiment

Soil properties	Results
Textural class	Clay loam
Sand (2–0.05 mm)	22.67%
Silt (0.05–0.002 mm)	41.58%
Clay (< 0.002 mm)	35.75%
pH	7.7
Electrical conductivity (EC)	4.09 dSm^{-1}
Soil organic carbon (SOC)	9.20 g kg^{-1}
Available soil N	0.60 g kg^{-1}
Olsen's extractable available P	0.04 g kg^{-1}
Available K	0.09 g kg^{-1}
Available S	0.04 g kg^{-1}
Available Na	0.21 g kg^{-1}
Easily extractable GRSP (EE-GRSP)	0.26 g kg^{-1}
Total GRSP (T-GRSP)	0.87 g kg^{-1}
Mean weight diameter (MWD)	0.32 mm

2.2 Experimental design

The pot experiment was established in February 2022. The duration of the experiment was 105 days. There were two treatments: (1) plant growing with AMF, and (2) plant growing without AMF as control treatment (NAMF). Each treatment was replicated five times and thus the total experimental pots were ten (10). All the pots (pot size 5 L) were filled with 2-mm sieved and autoclaved soil (4 kg pot^{-1}). The pots were arranged by following a complete randomized design (CRD). The fine roots (10 g fine roots pot^{-1}) of *Mangifera indica* L. and *Phyllanthus emblica* L. that were 74% and 52% colonized by AMF, respectively were added into five pots and considered as AMF treatments (Fig. S1). On the other hand, the sterilized fine roots (10 g fine root pot^{-1}) of the same plants were added into the remaining another five pots and considered as control. The treatments did not receive any synthetic fertilizers. Each pot was planted with four surface sterilized (70% ethyl alcohol) Okra seeds (*Abelmoschus esculentus*). After 15 days from the seed sowing, thinning was done and only a single plant was kept in each pot. Okra was grown over 105 days (February to June 2022) (Fig. S2). During the growing period, soil moisture was maintained at field capacity (water content at field capacity 38%) by irrigating every four days to replenish the soil moisture loss.

2.3 Plant and soil sample collection

After 105 days of okra cultivation, plant shoot and root were harvested. Fine root samples (un-dried) were collected to determine the AMF colonization status in both AMF and NAMF treated plant roots (Fig. S3). Plant shoot and remaining root samples were dried in an oven (65°C for 24 h) and weighed. The soil from each pot was poured on a separate polythene sheet then the larger particles were broken and passed through 4 and 0.25-mm sieves for wet sieving and chemical analysis, respectively. Oven dried plant samples were used for nutrient analysis.

2.4 Plant analysis

2.4.1 Measurement of AMF root colonization

Fine roots of *Mangifera indica* L., *Phyllanthus emblica* L., and *Abelmoschus esculentus* L. were stained by the methods proposed by Phillips and Hayman (1970). Briefly, the fresh root samples were washed with distilled water and preserved in 5% formalin. The preserved roots were washed with distilled water to remove the formalin and chopped into 1 cm pieces. Clean root samples were boiled in 10% KOH solution at 85–90 °C for 10 min in a water bath and the deeply pigmented roots were treated with 10% H_2O_2 at room temperature for 10 min. After washing with distilled water, the root samples were acidified with HCl (1%). Following that, the roots were stained with 0.05% aniline blue solution for 90 min at 90 °C temperature. Finally, the roots were destained and examined by a compound microscope at 10 × 10 magnification. The AMF colonization was evaluated by means of the intersection of quadrants method proposed by Giovannetti and Mosse (1980).

2.4.2 Plant nutrient analysis

The oven-dried plant samples were digested with HNO_3 and $HClO_4$ at a ratio of 2:1 in a closed microwave digestion system for the determination of P, K, and S concentration and the nutrient uptake was calculated by using plant dry matter (Huq and Alam 2005). The content K was measured with Flame Emission Spectrophotometer (Jenway, model-PFP7, UK). The S content in the plant extract was measured by the turbidity method proposed by Jackson (1973). The P content was determined by the vanadomolybdate yellow color method (Jackson 1973). Besides, plant N content was determined by Kjeldahl method (Page and Miller 1982).

2.5 Soil analysis

2.5.1 Soil physico-chemical properties analysis

The soil pH and electrical conductivity (EC) were measured with a soil: water ratio of 1: 2.5 and 1:5, respectively (Page and Miller 1982). Total soil N content was estimated by the Kjeldahl digestion technique (Page and Miller 1982). Soil available K was extracted by using a 1 N ammonium acetate ($CH_3CO_2NH_4$) solution (at pH = 7.0) at a ratio of 1:10 (Page and Miller 1982). After extraction, the concentration

was measured by an Atomic Absorption Spectrophotometer (AAS, Shimadzu model AA-7000, Tokyo, Japan). The available soil S was extracted by using potassium dihydrogen phosphate (KH_2PO_4) solution at a 1:10 ratio and was measured by the Turbidity method (Jackson 1973). Available soil P was extracted from the soil with 0.5 M sodium bicarbonate ($NaHCO_3$) at pH 8.5 (Jackson 1973), and the content was determined by the ascorbic acid blue color method (Murphy and Riley 1962).

2.5.2 Soil aggregate stability

Soil aggregate stability was measured by the wet sieving method proposed by Elliott (1986). Four following water-stable aggregates fractions were separated: (i) 4 − 2 (large macroaggregates), (ii) 2-0.25 (small macroaggregates), (iii) 0.25 − 0.053 (microaggregates), (iv) < 0.053 mm aggregates. Shortly, soil samples were immersed in the pure water for 5 min before moving the sieve up and down to about 3 cm depth for 50 times over 2 min. The fractions remaining on each sieve were collected and oven dried at 40 °C for 24 h and then weighed. The aggregate stability indicated by mean weight diameter (MWD) was calculated as:

$$MWD = \sum_{i=1}^{n} X_i W_i$$

Where X_i is the mean diameter of each aggregate fraction, W_i is the mass proportion of the aggregate fractions remaining on each sieve, and n is the number of fractions.

2.5.3 Soil organic carbon (SOC)

Soil OC in the bulk soil was estimated by following the Chromic acid wet oxidation method described by Walkley and Black (1934). Air-dried 2 g soil samples were oxidized with sulfuric acid (H_2SO_4) and potassium dichromate (K_2CrO_7). The unused chromic acid was titrated with ferrous sulfate ($FeSO_4$) solution to determine the SOC content.

2.5.4 Measurement of glomalin-related soil protein (GRSP)

The GRSP from soil samples was extracted using the method proposed by Wright and Upadhyaya (1996) and then the content was measured with the Bradford dye-binding assay, with bovine serum albumin as a standard. Briefly, for easily extractable glomalin-related soil protein (EE-GRSP), 0.25 g air-dried soil sample (< 2 mm) was placed into a centrifuge tube with 2 mL of 50 mM sodium citrate solution (pH = 8.0) and autoclaved for 30 min at 121 °C. After autoclaving, the supernatant was removed by centrifugation at 10,000 g for 5 min to remove the soil particles. After the extraction, supernatants were stored at 4 °C until further analysis. For total glomalin-related soil protein (T-GRSP), 0.25 g of < 2 mm air-dried soil was taken with 2 mL of 50 mM sodium citrate solution (pH = 8.0) and autoclaved for 90 min at 121 °C. After autoclaving, the supernatant was removed by centrifugation at 10,000 g for 10 min to remove the soil particles. This cycle was repeated five times until the supernatant showed colorless. Then, the supernatants were pooled together and stored at 4 °C for further analysis in a UV-visible spectrophotometer at 595 nm.

2.5.5 Soil microbial biomass carbon (MBC)

The MBC was determined by the chloroform fumigation extraction (CFE) method proposed by Vance et al. (1987). A 10 g of sample was divided into two portions. One portion was fumigated with ethanol-free chloroform ($CHCl_3$) for 24 h at 25 °C in the dark, while the other portion of the soil (non-fumigated) was extracted with 20 ml of 0.5 M potassium sulfate (K_2SO_4). The fumigated soils were also extracted with K_2SO_4 after 24 h of incubation. The organic carbon (OC) contents of the fumigated and non-fumigated soil extracts were measured using Walkley and Black's wet oxidation method (Walkley and Black 1934). The MBC was estimated from the difference in OC of the fumigated and non-fumigated soil extracts. Then OC was converted to MBC using an efficiency factor of 0.38 (Vance et al. 1987).

2.5.6 Fourier transform infrared (FTIR) analysis of SOM

The differences of C functional groups in SOM after AMF incorporation was evaluated by the FTIR spectrometer through the method described by Halder et al. (2023). The data of FTIR spectra were processed through Origin software (version 16.0) (OriginLab, USA). For all measured spectra, baseline and atmospheric corrections were made for H_2O and CO_2. The peak of phyllosilicate minerals was found at peak 3627 and 3628 cm^{-1} corresponded to the OH stretching (Bernier et al. 2013). The peak at 1759 cm^{-1} corresponding to the C-O stretching of ester was found (Parikh et al. 2014). The spectral region from 3000 to 2800 and 1740–1600 cm^{-1} corresponding to C–H and C = O stretching indicate the hydrophobic and hydrophilic region of whole soil. Parikh et al. (2014) suggested that the wettability of SOM is defined by these regions. The C-O-C stretching of polysaccharides were found in the region of 987–995 cm^{-1} (Poirier et al. 2005).

2.6 Statistical analysis

All the statistical analyses were performed by using SPSS 16.0. Shapiro-Wilk test was performed to test the data

normality. One-way analysis of variance (ANOVA) was used to explore the effects of AMF treatments on Okra shoot, root, fruit dry matter, uptake of nutrient (N, P, K and S), plant available soil nutrients (N, P, K and S), SOC, E-GRSP, T-GRSP, aggregate size distribution, MBC and MWD. The relationship among the plant dry matter, yield dry matter, MWD, SOC, EE-GRSP and T-GRSP, soil available N and P, their uptake in plants were described by the Pearson correlation matrix performed in MS excel 2016. The principal component analysis (PCA) was performed by using software R 3.6.1 (R Core Team 2018) to explore the potential impacts of AMF on Okra growth, nutrient uptake, and soil aggregation.

3 Results

3.1 Plant growth and nutrient uptake

In this study, AMF treatment significantly increased plant shoot, root, and fruit dry matter in comparison to NAMF ($p < 0.01$; Fig. 1). The shoot, root, and fruit dry matter of okra in AMF were increased by 32, 100, and 55% than NAMF, respectively ($p < 0.01$; Fig. 1). Moreover, mycorrhiza treatment significantly increased P, K and S assimilation in shoot, root and fruit ($p < 0.01$; Fig. 2; Table S1). Phosphorus uptake under AMF inoculation was increased by 4, 87, and 98% in shoot, root, and fruit, respectively in comparison to NAMF treatment ($p < 0.01$; Fig. 2; Table S1). In AMF treatments, K uptake in shoot, root, and fruit were raised by 1.45, 1.93, 1.97 times higher, while S uptake was improved by 183, 159, and 87%, respectively in comparison to control treatments ($p < 0.01$).

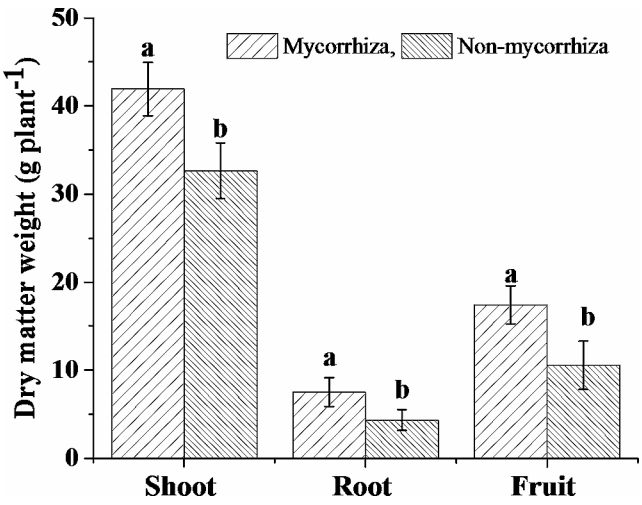

Fig. 1 Shoot, root and fruit dry matter of cultivated Okra under AMF and NAMF treatments. The vertical bar indicates standard deviation of the five replicates, $n = 5$. Different lowercase letters indicate significant difference between the AMF and NAMF treatments ($p < 0.01$)

3.2 Soil aggregation, soil organic carbon (SOC) and microbial biomass carbon (MBC)

Aggregate stability, measured as mean weight diameter (MWD) was found to be significantly higher (17%) in AMF treatments in comparison to NAMF ($p < 0.01$). The proportion of large macroaggregates (2-4-mm) and small macroaggregates (0.25-2-mm) in AMF treatments were increased significantly by 21 and 26% compared to NAMF treatments, respectively ($p < 0.01$; Fig. 3). In AMF treated soil, microaggregates were decreased by 6%, while no significant change of < 0.053 mm fraction was found. The SOC and MBC were increased significantly in the AMF treatment ($p < 0.01$; Table 2). The SOC was increased by 28%, while MBC was increased by 74% in AMF treatment than that of NAMF treatment ($p < 0.01$).

3.3 Functional groups of carbon in SOM

The FTIR spectra at 985–997 cm^{-1} corresponding to C– O – C stretching of polysaccharides was the dominant spectra among identified spectra of AMF and NAMF treatments (Fig. 4). The polysaccharide intensity was 1.15 times greater in the AMF treatment (peak showed at 992 cm^{-1}) than NAMF treatment (peak showed at 996 cm^{-1}).

3.4 The AMF colonization and glomalin-related soil protein (GRSP)

The AMF colonization in the AMF and control treatments were significantly different ($p < 0.001$). The hyphal colonization in AMF and NAMF treatments were 98 and 15%, respectively (Table 2). EE-GRSP and T-GRSP content were enhanced upon AMF incorporation in soil ($p < 0.01$; Table 2). The EE-GRSP content in the AMF and NAMF treatments were 0.53 and 0.32 g kg^{-1}, while the T-GRSP content were 1.56 and 1.13 g kg^{-1}, respectively (Table 2). Moreover, AMF treatment significantly increased the EE-GRSP and T-GRSP content in different aggregate fractions compared to NAMF except for < 0.053 mm fraction (Fig. 5a and b). In AMF treatment, the T-GRSP was increased by 44%, 37% and 23%, while the EE-GRSP was increased by 51%, 60% and 32% in comparison to NAMF in the 4 – 2, 2-0.25, 0.25–0.053 mm aggregate fractions, respectively ($p < 0.01$; Fig. 5a and b). In addition, EE-GRSP and T-GRSP content in the macroaggregates except for small macroaggregates of NAMF under EE-GRSP were enhanced significantly compared to other aggregates fractions ($p < 0.01$; Fig. 5a and b).

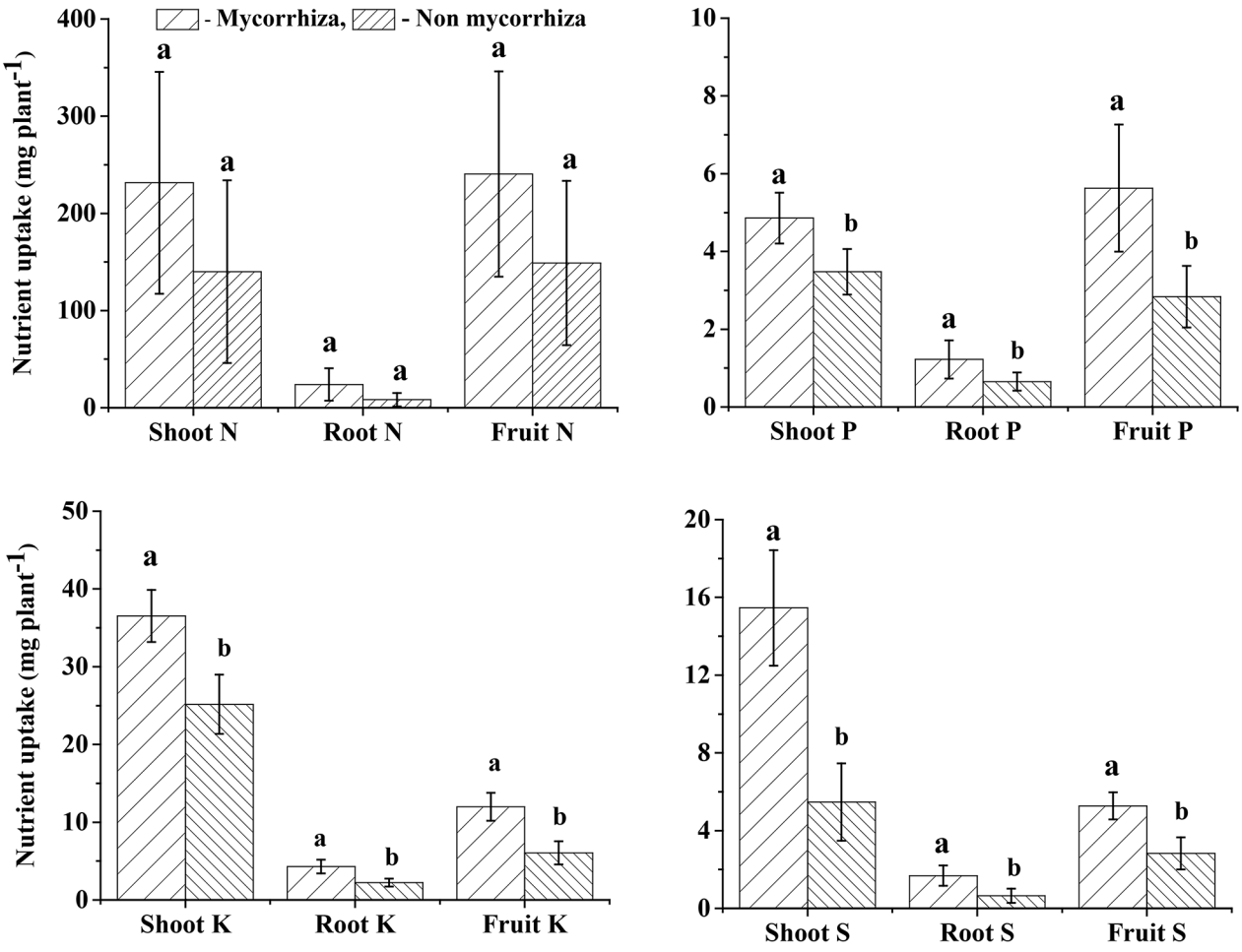

Fig. 2 Plant nutrient uptake in shoot, root, and fruit parts under AMF and NAMF treatments. The vertical bar indicates standard deviation of the five replicates, $n = 5$. Different lowercase letters indicate significant difference between the same plant parts under AMF and NAMF treatments ($p < 0.01$)

3.5 Soil nutrient availability

The available soil N, P, K and S were increased by AMF treatments (Fig. 6; Table S1). The availability of P and K content were enhanced from 0.05 to 0.08 and 0.20 to 0.27 g kg^{-1}, respectively, while available N content in AMF was increased by 1.17-fold higher than NAMF upon AMF application ($p < 0.01$; Table S1).

3.6 Principal component analysis and correlation among the variables

Okra shoot, root, and fruit biomass production were significantly correlated with aggregate stability and macro-aggregation, while nutrient uptake was significantly correlated with AMF colonization and aggregate stability rather than nutrients availability (Fig. S4, 7a, 7b and Table 3). On the other hand, soil aggregate stability and macroaggregates correlated with AMF colonization and GRSP (EE-GRSP and T-GRSP) (Table 3 and Fig. S4 and 7a).

The PCA (variable and biplot PCA) was performed on the nutrient uptake parameters in different plant parts (N, P, K and S), yield parameters (SB, RB and FB) with soil physical and chemical properties as influenced by AMF (Fig. 7a). The first two principal components (PCs) reflect the most variability, accounting for 84% of the variance of the dataset, with PC1 and PC2 accounting for 72.8% and 11.2% of the total variance, respectively. The highest contribution was made by the AMF, MWD, FB, RB while the least was contributed by the SOC, TGRSP, and MBC (Fig. 7a). The AMF and NAMF treatments were clustered independently in the PCA (Fig. 7b), indicating, the AMF had consistent and distinct effects across the dependent variables.

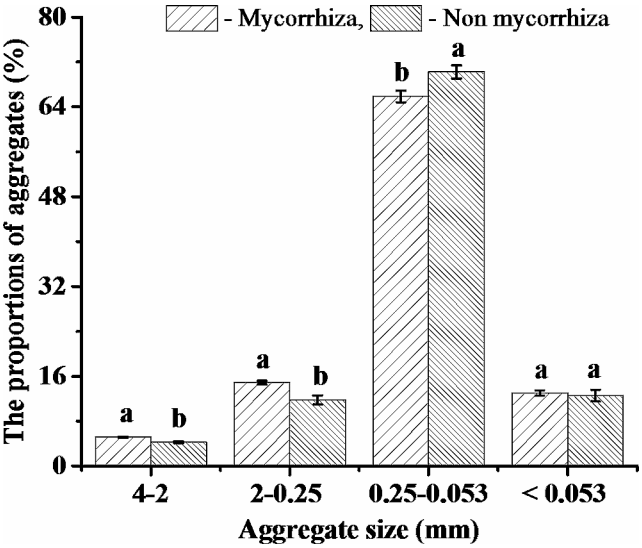

Fig. 3 Soil aggregate size distribution under AMF and NAMF treatments. The vertical bar indicates standard deviation of the five replicates, $n=5$. Different lowercase letters indicate significant difference between the same aggregate fractions of AMF and NAMF treatments ($p<0.01$)

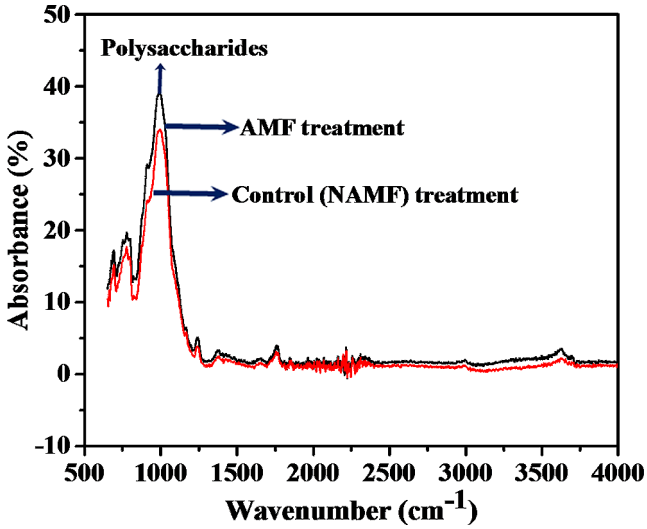

Fig. 4 Fourier transform infrared (FTIR) spectra of SOM under AMF and NAMF (control) treatments

4 Discussion

4.1 Effect of AMF on plant growth and nutrient uptake

In our present short-term pot experiment, AMF treatment

Table 2 Aggregate stability (MWD), soil organic carbon (SOC), easily extractable glomalin-related soil protein (EE-GRSP), total glomalin-related soil protein (T-GRSP), and microbial biomass carbon (MBC) following AMF and NAMF treatment

Treatment	MWD (mm)	SOC (g kg^{-1})	EE-GRSP (g kg^{-1})	T-GRSP (g kg^{-1})	MBC (g kg^{-1})	Hyphal colonization (%)
AMF	0.41 ± 0.01a	11.7 ± 0.9a	0.53 ± 0.07a	1.56 ± 0.19a	1.44 ± 0.36a	98 ± 6a
NAMF	0.35 ± 0.01b	9.1 ± 0.9b	0.32 ± 0.10b	1.13 ± 0.17b	0.83 ± 0.33b	15 ± 1b

In each column, values are means ± SD (standard deviation), $n=5$. Different lowercase letters within the same column indicate significant difference between the treatments ($p<0.01$)

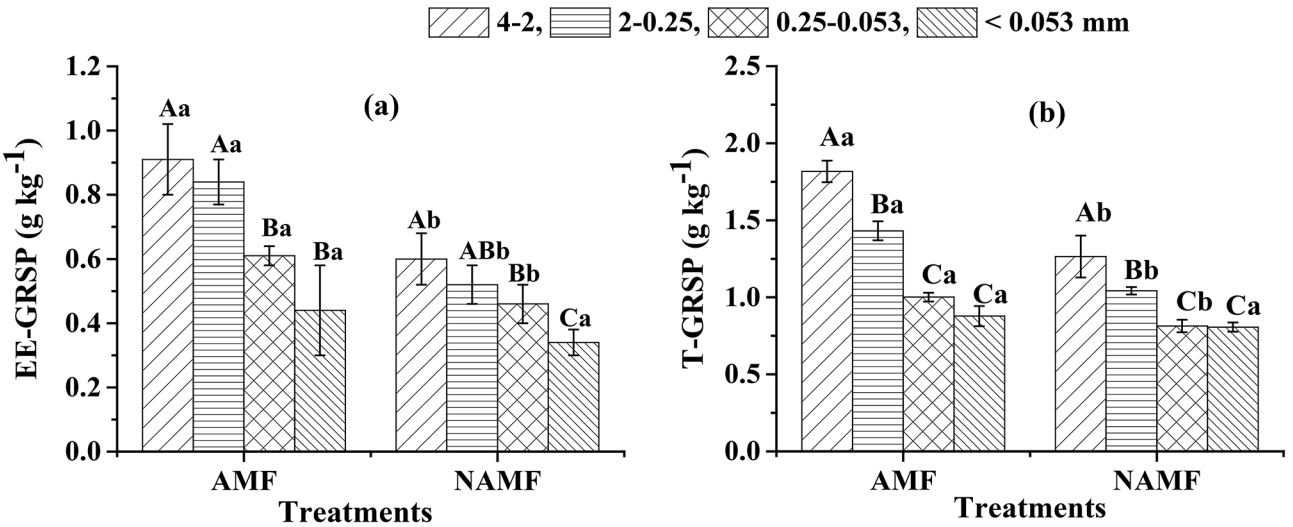

Fig. 5 EE-GRSP (a) and T-GRSP (b) contents in different soil aggregate fractions following AMF and NAMF treatments. The vertical bars indicate the standard deviation of five replicates, $n=5$. The different lowercase letters indicate significant difference between the treatments of same aggregate fractions ($p<0.01$), while the different uppercase letters indicate significant difference among the different size aggregates under the same treatment ($p<0.01$)

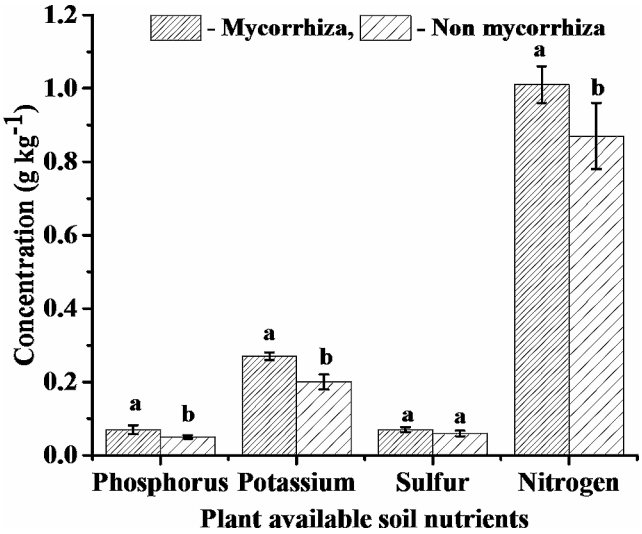

Fig. 6 Plant available soil phosphorous (P), potassium (K), and sulfur (S) content following AMF and NAMF treatment. The vertical bar indicates standard deviation of the five replicates, $n = 5$. Different lowercase letters indicate significant difference between the AMF and NAMF treatments ($p < 0.01$)

improved the growth and productivity of Okra compared to NAMF treatment ($p < 0.01$). The current result was consistent with the previous study regarding the impacts of AMF treatments on plant growth and productivity (Halder et al. 2015b; He et al. 2019; Wang et al. 2021; Eltigani et al. 2022). Eltigani et al. (2022) reported that mycorrhiza treatments significantly increased the plant biomass in five different Okra cultivars under a greenhouse experiment in Germany. Wang et al. (2021) found that AMF enhanced the root biomass, aboveground biomass, and grain yield under both types of experiments (the pot and field) in China. Tanwar et al. (2013) reported that AMF stimulates the chlorophyll content in leaves, and the photosynthetic efficiency of plants, which eventually increases the host plant productivity and biomass accumulation. In our present study, okra growth and nutrient uptake were increased after AMF application (Figs. 1 and 2), which might be correlated to the soil aggregation and microbial biomass production in AMF treatment (Table 3; Fig. 7a). Soil aggregation facilitates plant growth and productivity through improving water and air transportation, root growth and function, nutrient availability, and microbial activity (Bronick and Lal 2005). Soil aggregation promotes plant productivity increasing soil porosity, C sequestration, water, and nutrients retention (Le Bissonnais 1996). A good aggregated soil easily facilitates movement of dissolve nutrients among the pore space of aggregates and their subsequent uptake in plants (Balesdent et al. 2000a; Oades 1984). Soil aggregates enhance the soil C stabilization, acts as a source of nutrients for plants within the soil aggregates, and reduce nutrients loss protecting soil erosion (Bronick and Lal 2005). Bedel et al. (2018) and Zhang et al. (2022) found that aggregate stability is the indicator of mineral nutrients like N, K, Ca and Mg availability. Chen et al. (2023) suggested that soil aggregation increases the soil-available N and P and thereby leading to higher uptake and vegetative growth. Soil aggregate stability increases the soil nutrients accumulation by enhancing non-capillary porosity, cation adsorption, and microbial function (Bai et al. 2018). In addition, AMF synthesize organic acids (carboxylates such as citrate and malate) as root exudation, which dissolve the Al- and Ca-phosphates and thus increase the availability of inorganic P (Vance et al. 2003; Pang et al. 2015; Klugh-Stewart and Cumming 2009). As a result, plants uptake this readily available P from the root zone and thereby leading to increase the P content in plant biomass (Schachtman et al. 1998; Smith and Smith 2011).

4.2 AMF and aggregate stability

In our study, AMF incorporation increased the MWD significantly than NAMF, which was largely contributed by AMF colonization (Table 3; Fig. 7a). The result was corroborated with the previously published reports (Quilliam et al. 2010; Olsson et al. 2014; Wu et al. 2015; Xu et al. 2015). Wu et al. (2015) reported that AMF significantly increased macroaggregates formation and thus MWD under a pot experiment conducted in Udic Ferralsols. Xu et al. (2015) found that MWD was increased with AMF treatments under tomato (*Solanum lycopersicum* L.) and maize (*Zea mays* L.) in the lime concretion black soil. Avio et al. (2006a) reported that the hyphal density and length of AMF strongly contribute to the improvement of aggregate stability. In the current study, MWD enhancement was significantly contributed by AMF hyphal colonization ($r = 0.96$; $p < 0.001$) followed by SOC ($r = 0.86$; $p < 0.01$) and GRSP ($r = 0.78$; $p < 0.01$ and $p < 0.72$) (Table 3). AMF inoculation significantly increased the AMF hyphal network and thereby leading to increase the MWD by enmeshing and entangling the soil particles (Tisdall 1991; Avio et al. 2006a). Wessels (1999) and Chenu and Stotzky (2002) suggested that the tunneling mechanism of AMF hyphae can align the clay particles along growing hyphae. These hyphae can exert considerable pressure on adjacent soil particles and organic matter to press them together, and thereby leading to increased MWD (Money 1994). Tisdall (1991) suggested that fungal hyphae act as a transient binding agent, entangle the soil particles and increase the stability of aggregates. Staddon et al. (2003) found that AMF hyphae can turn over rapidly about 5– 6 d, while runner hyphae of ecto-mycorrhiza can stabilize soil aggregates for an average up to 11 months (Treseder et al. 2005).

Gryndler et al. (2009) suggested that the greater SOC is a result of decomposition products and secondary metabolites

Table 3 Correlation among the soil properties, plant dry matter, and plant nutrient uptake

	SB	RB	SNU	FNU	SPU	FPU	AMF	MWD	EEGRSP	TGRSP	SOC	MBC	AN	AP	LMA	FB
SB	1	0.93***	0.78**	0.58	0.75*	0.67*	0.68*	0.71*	0.66*	0.49	0.35	0.42	0.41	0.33	0.71*	0.78**
RB		1	0.85**	0.62	0.86**	0.77**	0.81**	0.82**	0.76*	0.59	0.54	0.55	0.52	0.42	0.80**	0.80**
SNU			1	0.71*	0.85**	0.86**	0.77**	0.74*	0.66*	0.85**	0.51	0.51	0.66*	0.42	0.70*	0.94***
FNU				1	0.44	0.55	0.49	0.51	0.36	0.57	0.04	-0.03	0.46	0.21	0.33	0.48
SPU					1	0.83**	0.77**	0.74*	0.78**	0.62	0.63*	0.72*	0.51	0.55	0.79**	0.81**
FPU						1	0.76*	0.72*	0.80**	0.76*	0.54	0.36	0.36	0.57	0.87**	0.88**
AMF							1	0.96***	0.83**	0.77**	0.83**	0.70*	0.74*	0.81**	0.89**	0.83**
MWD								1	0.78**	0.72*	0.83**	0.62	0.66*	0.80**	0.87**	0.78**
EEGRSP									1	0.46	0.59	0.49	0.31	0.73*	0.86**	0.66*
TGRSP										1	0.66*	0.48	0.78**	0.54	0.67*	0.90***
SOC											1	0.80**	0.60*	0.76*	0.77**	0.58
MBC												1	0.72*	0.52	0.60	0.52
AP													1	0.47	0.44	0.58
AN														1	0.44	0.68*
LMA															1	0.81**
FB																1

Here, SB- Shoot biomass, RB- Root biomass, SNU- Shoot nitrogen uptake, FNU- Fruit nitrogen uptake, SPU- Shoot phosphorus uptake, FPU- Fruit phosphorus uptake, AMF- Arbuscular mycorrhiza fungi colonization, EEGRSP- Easily extractable glomalin related soil protein, TGGRSP- Total glomalin related soil protein, SOC- Soil organic carbon, MBC- Microbial biomass carbon, AN- Available nitrogen, AP- Available phosphorus, LMA- Large macroaggregates, FB- Fruit biomass*, **, *** indicate correlation significant at 0.05, 0.01, 0.001 level

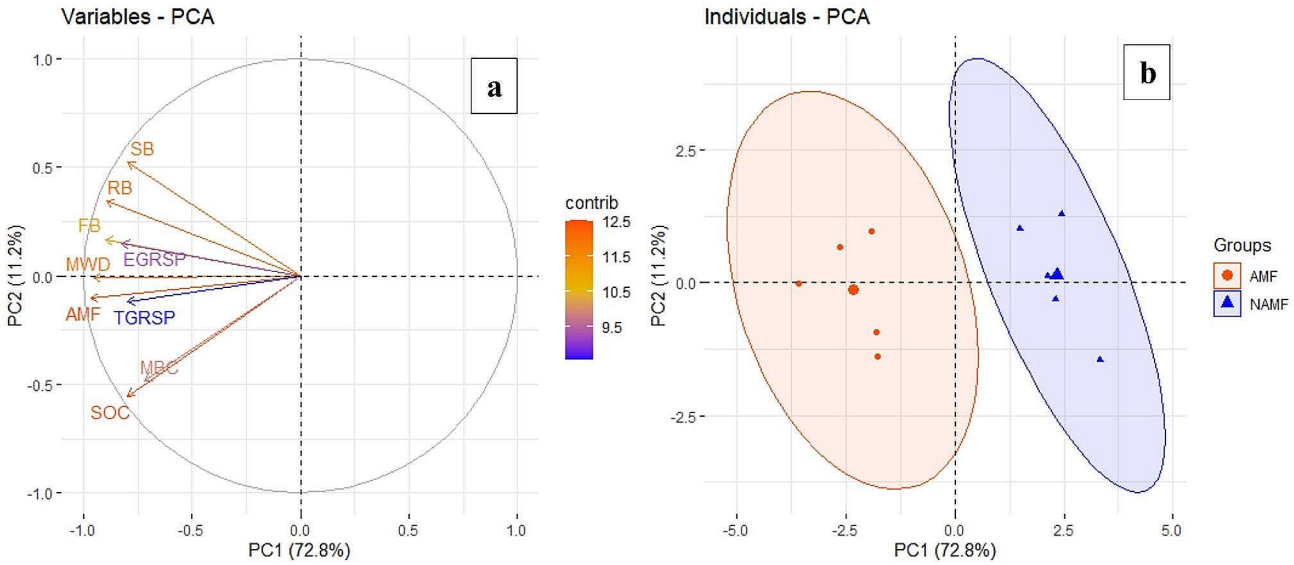

Fig. 7 The principal component analysis diagram (variable PCA; **(a)** and individual PCA; **(b)**) shows how AMF affects plant biomass production and the characteristics of the soil. The stronger the correlation between these dependent variables, the bigger the loading and the smaller the angle among the vectors in variable PCA. The higher contribution is represented by the color red, while the smaller contribution is shown by the color blue. The variable includes shoot biomass: SB, root biomass: RB, fruit biomass: FB, arbuscular mycorrhiza colonization (AMF), aggregate stability (MWD), soil organic carbon (SOC), microbial biomass carbon (MBC), extractable glomalin-related soil protein (EGRSP), total glomalin-related soil protein (TGRSP)

synthesized during decomposition by the enhanced soil microbial community after AMF treatments (Table 2). Xu et al. (2018) found that photosynthetic C substrate is incorporated into soil as additional C upon AMF treatments in exchange of mineral nutrients to plant roots. Graham (2000) suggested that AMF receive between 4 and 20% of total plant photosynthate and finally added to the soil as additional C. According to Finlay and Soderstrom (1992), AMF have direct access to C that has been fixed by host plants, and they disperse this C throughout the rooting zone's soil for use by soil microbes. Chenu (1989) found that fungus inoculation enhances the synthesis of polysaccharides in soil, while Caesar-TonThat and Cochran (2000) highlighted the fungal-derived mucilage (Fig. 4). These microbial secretions increase the SOC and thus their considerable gluing action increases the soil aggregation (Chenu 1989; Caesar-TonThat and Cochran 2000).

Rillig and Mummey (2006) and Wu et al. (2014) pointed out the significance of GRSP coupling with hyphal colonization for aggregation. We also found considerable impacts of GRSP coupling with AMF colonization on aggregation (Table 3; Fig. 7a). Glomalin-related soil protein (GRSP), a fungal protein, is found tightly bound with AMF hyphae and spore walls (Wright and Upadhyaya 1996; Rillig 2004; Rillig and Mummey 2006), plays a key function in increasing the water stability of soil aggregates by gluing the soil particles together (Rillig and Mummey 2006; Yang et al. 2022). Fall et al. (2022) found that the hydrophobic nature of glomalin contributes to increasing the aggregates resistant to water slaking. Furthermore, the soil GRSP is considered a novel bio-flocculant, which is rich in Fe (Fe^{2+} and Fe^{3+}), K^+, Ca^{2+}, Mg^{2+}, Zn^{2+}, Cu^{2+}, Mn^{2+} (Rillig et al. 2001; Weber et al. 2006; Chern et al. 2007). These cations significantly enhance the biogeochemical process such as the flocculation of soil particles (Zheng et al. 2018). Moreover, Fe of GRSP participates in the bridging mechanism between GRSP and soil mineral particles (Wang et al. 2021). The bridging mechanism of GRSP is controlled by their different functional groups and higher molecular weight, which provides more binding sites for flocculation and aggregation (Yuan et al. 2011; Lehmann et al. 2020). The GRSP consists of the hydroxyl (-OH), carboxyl (-COO-), carbonyl (C = O), amide (-CO-NH), and primary amine ($-NH_2$) functional groups (Wang et al. 2021). The above-mentioned functional groups of GRSP are the major determinant for bridging mineral particles to form large flocs during aggregation (Yuan et al. 2011). We found that GRSP fractions were increased with aggregate size and the result was supported by Han et al. (2023), who found that soil GRSP fractions improved with increasing the size of soil aggregates. GRSP binds smaller soil mineral particles to micro-aggregates to stable macro-aggregates by following the aggregates hierarchy leading to greater GRSP in the macroaggregates (Tisdall and Oades 1982; Lehmann et al. 2020). Driver et al. (2005) suggested that higher GRSP accumulation in the soil macroaggregates was contributed by AMF hyphae. The primary pathways of

GRSP accumulation in soil are AMF hyphal turnover and then the GRSP is released from dead mycelium (Driver et al. 2005). AMF hyphae can turnover very rapidly, calculated half-life were 5–6 days, thereby leading to greater GRSP accumulation in macroaggregates (Staddon et al. 2003).

5 Conclusion

AMF increased the root, shoot, and fruit dry matter of Okra in comparison to NAMF. Soil macronutrients as N, P, K and S availability were enhanced upon AMF inoculation. Furthermore, AMF increased the uptake of N, P, K, and S in the root, shoot and fruit biomass of Okra. Soil aggregation, GRSP, SOC, and microbial biomass were also improved upon AMF inoculation. Okra growth and productivity were potentially linked with macroaggregate formation thus stability of soil aggregates, while aggregate formation was linked with AMF hyphal colonization followed by SOC and GRSP following AMF hyphal turnover. Our findings demonstrate that integrating AMF in crop cultivation is an effective strategy to improve soil condition and plant growth that paves the way for sustainable management of arable soils.

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Author contributions Data collection and laboratory analysis were undertaken by Shova Akter. All authors contributed to preparation of manuscript.

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Data availability The datasets used in the current study are available from corresponding author upon reasonable request.

Declarations

Competing interests The authors declare that there is no potential of competing interests that could have influence the study reported in this article.

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