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Mitigating the effects of water-deficit stress on potato growth and photosynthesis using mycorrhizal fungi and phosphate-solubilizing bacteria

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Abstract

Biofertilizers, such as arbuscular mycorrhiza fungi and phosphate-solubilizing bacteria (PSB), have been reported to enhance plant growth under water stress conditions. This study aimed to investigate the effect of different biofertilizers on potato photosynthesis and growth under water deficit stress. The experiment was conducted over two crop years (2019 and 2020) using a randomized complete block design with three replications. Four irrigation intervals (70, 90, 110 and 130 mm of cumulative evaporation) and six biofertilizer treatments (PSB, *Funneliformis mosseae* [FM], *Rhizoglomus fasciculatum* [RF], PSB + FM, PSB + RF and no use) were applied. Severe moisture stress (130 mm evaporation) compared to no stress (70 mm evaporation) increased substomatal carbon dioxide concentration. The application of biofertilizers improved tuber yield under severe moisture stress, with FM showing the highest increase (62.9%), followed by RF (59.8%) and PSB (48.4%). The use of PSB along with mycorrhizae led to a significant decrease in mycorrhizal colonization percentage at all irrigation levels. The highest percentage of colonization and net photosynthesis was obtained from the application of both mycorrhizal species under irrigation conditions after 70 mm of evaporation. The application of PSB alone resulted in a 14.6% increase in the transpiration rate, additionally, the use of mycorrhiza led to an 18.7% increase in stomatal conductivity compared to no-biofertilizer. The results suggest that the simultaneous use of PSB and mycorrhizae can be effective in mild moisture stress, but in severe moisture stress, the use of mycorrhizal species alone is more effective.

Introduction

Potato (*Solanum tuberosum* L.) is the world's third most consumed crop after rice and wheat, with a global production of over 360 million tons annually (FAO, 2020). In 2020, Iran produced 4.47 million tonnes of potato, with Hamedan province being the largest producer, accounting for over 23% of the total production (Agricultural Statistics, 2020; Dadrasi *et al.*, 2022*a*, 2022*b*). Potato requires optimal irrigation to achieve proper growth and tuber yield, as it has a high amount of water requirement (Steyn *et al.*, 2016). Drought stress can decrease or halt physiological activities, including growth, transpiration, photosynthesis and cellular enzyme activity (Song, 2005). Stomatal conductance is a critical physiological factor that affects photosynthesis, and it is a suitable index for evaluating photosynthesis activity under drought stress conditions. Previous studies have shown that reducing plant relative water content due to drought stress can decrease stomatal conductance, net photosynthesis and carbon dioxide assimilation (Yujie and Lizhong, 2015). Drought stress can also diminish photosynthesis by reducing protoplasmic activity and carbon dioxide stabilization, as well as protein and chlorophyll synthesis (Jarosław *et al.*, 2020). Drought stress can reduce leaf area index (LAI) in potato cultivars, as reported by Khosravifar *et al.* (2020), due to reduced cell turgor and division, leading to reduced leaf area expansion (Mai *et al.*, 2018). In conditions of soil moisture deficiency, nutrient absorption, particularly phosphorus, is reduced (Dibenedetto *et al.*, 2017). Moreover, the mobility and absorption of phosphorus is greatly reduced in calcareous soils, which are prevalent in Iran (Salimpour *et al.*, 2010). Previous research suggests that the use of microorganisms, which can increase phosphorus absorption by roots, can improve plant tolerance to moisture stress (Abdel-Fattah and Shakry, 2016; Ray and Lakshmanan, 2020). Arbuscular mycorrhizal fungi (AMF) and phosphate-solubilizing bacteria (PSB) are beneficial microorganisms that promote plant growth through various mechanisms, including metabolic adjustments, phytohormone regulation and enhancement of nutrient availability (Evelin *et al.*, 2009; Muhammad *et al.*, 2017; Khan *et al.*, 2021). These microorganisms can also induce plant resistance to biotic and abiotic stresses, such as pathogen attack and heavy metal contamination (Muhammad *et al.*, 2017; Mustafa *et al.*, 2019; Ray and Lakshmanan, 2020). The application of biofertilizers has been shown to increase shoot biomass and potato tuber yield, attributed to efficient nutrient use (Dash and Jena, 2015). Drought stress reduces LAI in potato cultivars due to reduced cell turgor and division, leading to reduced leaf area expansion (Mai *et al.*, 2018; Khosravifar *et al.*, 2020). Soil moisture deficiency reduces nutrient absorption, particularly phosphorus, which is further reduced in calcareous soils prevalent in Iran (Salimpour *et al.*, 2010; Dibenedetto *et al.*, 2017). Microorganisms that increase phosphorus absorption by roots can improve plant tolerance to moisture stress (Abdel-Fattah and Shakry, 2016; Ray and Lakshmanan, 2020). PSB can increase phosphorus availability and root growth (Farzana and Radizah, 2005; Bashir *et al.*, 2017). Different mycorrhizal species have varying effects on potato tuber yield and plant response to environmental conditions (Bayrami *et al.*, 2012). AMF have been effectively inoculated in various crops, such as cotton, tomato, pepper, bean, garlic, soybean, cucumber, melon, watermelon, corn and eggplant (Ortas, 2012). Gai *et al.* (2006) reported that several AMF species can successfully inoculate sweet potatoes to different degrees. Mycorrhizae enhance root system growth by modulating plant hormones and indirectly increase access to inactive nutrients through improved root system area (Marschner, 2011). While many studies have investigated the use of AMF to mitigate the effects of drought stress in various plants, few studies have been conducted on potato (Zhao *et al.*, 2015). Reports suggest that PSB isolates can significantly improve growth parameters, photosynthesis and NPK concentration in plants, outperforming the control (Dawwam *et al.*, 2013). Dual inoculation with both mycorrhiza and bacteria has been shown to stimulate plant growth more effectively than single inoculation with either microorganism alone (Singh and Kapoor, 1998; Nacoon *et al.*, 2020). PSB can solubilize P, which is then taken up and delivered to the plant by AMF, explaining the interactive (synergistic) effects of the two microorganisms (Ordoñez *et al.*, 2016). Due to the high-water demand of potato and the limited availability of irrigation water, utilizing AMF and PSB could potentially enhance potato growth under moisture stress conditions. This study aimed to investigate the effects of AMF and PSB on several photosynthetic parameters, physiological indices and tuber yield of a common potato cultivar grown in Hamedan, Iran.

Materials and methods

The experiment was conducted over 2 years, in 2019 and 2020, at the Ekbatan agriculture research station in Hamedan province, Iran. The research site was located at an altitude of 1730 m above sea level, 34°52′46″ N latitude, and 48°32′13″ E longitude. The results of the soil test conducted are presented in Table 1, while the weather conditions during the two growing seasons are shown in Table 2. Based on the weather conditions in the study area, the potato seeds were sown on 15 June, and harvesting was done on 2 October in 2019. In 2020, the sowing and harvesting times were 9 June and 29 September, respectively.

The experiment was designed as a randomized complete block factorial design with three replications. The study involved two factors: irrigation levels (at 4 levels, i.e. irrigation after 70 [I1], 90 [I2], 110 [I3] and 130 [I4] mm of cumulative evaporation from class A evaporation pan) and biofertilizer (at 6 levels, i.e. PSB, mycorrhiza of *Funneliformis mosseae* [FM], mycorrhiza of *Rhizoglomus fasciculatum* [RF], PSB + FM, PSB + RF and control). The control treatment's cumulative evaporation amount (70 mm) was determined based on the lysimeter experiment results. The research plots had different areas for each cropping year and consisted of four rows of potato plants, each 7 m long. The potato cultivar used was Marfona, with a planting density of 53 000 plants per hectare and a row spacing of 75 cm. Based on the soil test results (Table 1), 100 kg/ha of phosphate fertilizer was applied, obtained from triple superphosphate and placed in 5 cm deep strips below the seeds. The recommended amount of nitrogen (180 kg/ha) was applied in a strip along the planting lines in two stages: planting and flowering at stage 51 of BBCH (Biologische Bundesarstalt, Bundessoztenamt and Chemical scale) (Kacheyo *et al.*, 2020). The mycorrhizal biofertilizers used in the experiment were prepared from plant roots containing hyphae of two types of fungi obtained from Turan Biotechnology Company. The inoculum contained an estimated number of fungal spores between 50 and 150 per gram, and the recommended amount of inoculum was 20 g/m^2 as per the manufacturer's instructions. The potato seeds required for each experimental plot were determined, and they were moistened before evenly pouring 420 g of inoculum on them. The PSB biofertilizer used in the experiment contained *Pseudomonas putida* strain P13 and *Pantoea agglomerans* strain P5 bacteria, with 10^9 colony-forming unit of PSB per gram. This biofertilizer is produced by the Green Biotechnology Company and is available in 100 g packages, suitable for one hectare of crops. To ensure the activity of PSB, a solid medium containing tricalcium phosphate supplemented with bromophenol blue was used (Nautiyal, 1999; Pande *et al.*, 2017). The bacteria were incubated at 28°C for 5 days, and the formation of a clear halo around the bacteria was considered a sign of their activity (Chen *et al.*, 2006).

To apply PSB, the potato seeds were first placed in the shade on a clean surface. The inoculum powder containing PSB was then dissolved in an appropriate amount of chlorine-free water, filtered with a cloth and evenly sprayed on the seeds. After drying in the shade, the potato seeds were planted. In treatments where both types of biofertilizers were used, PSB was first inoculated, followed by mycorrhizae. Weed control in the experimental field was carried out manually at four growth stages of potato: five leaves (stage 15 of BBCH), stem elongation (stage 22 of BBCH), beginning of crop cover (stage 31 of BBCH) and before flowering (stage 51 of BBCH) (Kacheyo *et al.*, 2020). A yellow card was used in the field to control pests.

Table 1. Physical and chemical characteristics of soil experimental field at 0–30 cm depth

Year	EC (dS/m)	pH	OC (%)	P (mg/kg)	K (mg/kg)	N (%)	Clay (%)	Silt (%)	Sand (%)	Soil texture
2019	0.45	7.72	0.54	3.4	385	0.05	14.5	26.5	59.0	Sandy Loam
2020	0.77	7.60	0.50	3.8	437	0.05	10.5	36.0	53.5	Sandy Loam

EC, electrical conductivity; OC, organic carbon; P, phosphorus; K, potassium; N. nitrogen.

Table 2. Weather characteristics during two growing seasons (2019 and 2020)

Month of the growing season	Minimum temperature (°C)	Average temperature (°C)	Maximum temperature (°C)	Precipitation (mm)
2019				
June	12.3	22.4	32.4	13
July	14.7	25.1	35.5	0
August	15.8	25.7	35.5	1
September	10.5	21.2	31.8	0
October	6.9	16.6	26.2	0
2020				
June	10.2	20.6	31.1	19
July	13.9	23.4	33	0.1
August	14.9	24.2	34.5	0
September	9.5	20.2	30.8	0
October	5.4	15.4	25.4	0

Irrigation was performed using drip tapes, and soil sampling was conducted 1 day before irrigation to determine the percentage of weight moisture from the depth of root development. The soil samples were dried in an oven at 104°C for 24 h. It is worth noting that deficit irrigation based on the treatments was initiated after the plants had fully established, i.e. at the beginning of canopy closure (stage 30 of BBCH). The amount of water required in each irrigation session was determined using Eqn (1) (Alizade, 2001).

$$d = (\mathrm{Fc} - \mathrm{P0}) \times \mathrm{As} \times D/100 \qquad (1)$$

The amount of water required for each irrigation session was calculated using Eqn (1), where d represents the water height in cm, Fc is the percentage of soil moisture by weight at the field capacity stage (28.6%), P0 is the percentage of soil moisture by weight at the time of irrigation, As denotes the soil bulk density (1.44 g/cm^3) and D refers to the depth of root development (30 cm) multiplied by 100 to obtain the amount of water in cubic meters per hectare. The water consumption per hectare for each irrigation level is presented in Table 3. Water productivity was calculated by dividing the tuber yield by the amount of water used in irrigation, following the method of Briggs and Shantz (1913).

The maximum LAI was measured using grid paper during the flowering stage (stage 60 of BBCH) (Villa *et al*., 2017; Kacheyo *et al*., 2020). LAI was calculated as the ratio of the measured leaf area of the plant to the ground area (Watson, 1947). Furthermore, the amount of chlorophyll a and b was measured according to the Arnon method (1967).

To measure the maximum dry weight, the aerial parts and tubers of five plants (at stage 88 of the BBCH scale) (Kacheyo *et al*., 2020) were placed in an oven at 70°C for 3 days and then weighed with an accuracy of 0.01 g. Also, to determine the percentage of phosphorus in potato tuber ash, the vanadomolybdate reagent and standard phosphate solutions were utilized at a wavelength of 420 nanometers by a spectrophotometer (Murphy and Riley, 1962).

Photosynthetic parameters were measured using an Infrared Gas Analyzer (IRGA) model CI-340 (made in the USA) on an open system from 9 to 11 AM at the time of flowering. For this purpose, the third developed young leaf from the top of the plant was selected and placed inside a special chamber for broad leaf plants to cover the entire chamber and make full use of sunlight. Gas exchange was measured on three plants in each test plot when the plant reached the maximum LAI (stage 60 of BBCH) (Villa *et al*., 2017).

The gas exchange characteristics of the leaves were measured, including transpiration rate (mmol $H_2O/m^2/s$), stomatal conductance (mol $CO_2/m^2/s$), sub-stomatal carbon dioxide concentration (μmol/mol) and net photosynthetic rate (μmol $CO_2/m^2/s$). Mesophilic conductivity was also obtained by dividing the rate of net photosynthesis by sub-stomatal carbon dioxide concentration (Fischer *et al*., 1998).

To determine the percentage of root mycorrhizal colonization, root sampling was performed on five plants at the stage of tuber formation (stage 40 of BBCH) (Kacheyo *et al*., 2020), and root staining was performed using the method of Phillips and Hayman (1970). The percentage of root colonization was calculated using the method of intersecting grid lines (Dalp, 1993). Tuber yield was determined by completely harvesting an area of 3 m^2 when 50% of the leaves turned brown (stage 95 of BBCH). After collecting the data and checking the normality of the residuals, a combined analysis was performed using SAS software ver. 9.4, and graphs were drawn using Excel software. Regression relationships were determined between measured traits and irrigation intervals for each biofertilizer treatment (in cases where the biofertilizer × irrigation interval interaction was

Table 3. The volume of water used at different levels of irrigation (70, 90, 110 and 130 mm) in 2019 and 2020 based on weather condition

	Volume of water (m^3/ha)	
Irrigation levels (mm cumulative evaporation from class A evaporation pan)	First year	Second sear
70	6502	6211
90	5624	5202
110	4798	4423
130	3956	3608

statistically significant) and plotted using the SAS Nline procedure. Mean comparisons were conducted using Duncan's method at the 5% probability level.

Results

Colonization and tuber phosphorus

The analysis of variance results indicated that the main effects of the investigated factors (year, irrigation interval and biofertilizer) on AMF colonization percentage and tuber phosphorus percentage were highly significant. All two-way interactions had significant effects on AMF colonization, but tuber phosphorus percentage was only influenced by the two-way interaction of biofertilizer × irrigation interval (Table 4).

Mean comparison for the two-way effect of biofertilizer × year (Fig. 1) indicated that the highest percentage of colonization in all treatments was obtained in the second year of the experiment. In all biofertilizer treatments (except for the only bacteria and the control), the percentage of AMF colonization in the second year was about 30% higher than in the first year of the study (Fig. 1). However, the highest tuber phosphorus percentage was recorded in the first year (0.41%), which was 7.8% higher compared to the second year. The percentage of root colonization decreased linearly with an increase in cumulative evaporation while the tuber phosphorus percentage increased with increasing moisture stress intensity (Table 5). The highest percentage of tuber phosphorus is achieved in irrigation after 130 mm of evaporation, particularly when applying FM or the combination of PSB with both mycorrhizal species (Table 6). The highest slope of decrease in colonization with increasing moisture stress intensity was observed with the application of RF, while the lowest slope in tuber phosphorus percentage increase with increasing moisture stress intensity was again observed with the application of RF (Table 5). It was found that the use of AMF alone led to an increase in the percentage of root colonization. No significant difference was observed between the two AMF species at all irrigation levels, except for the irrigation treatment after 90 mm of evaporation, where *R. fasciculatum* (RF) showed 5.3% more colonization than *F. mosseae* (FM) (Table 6). According to the results, there is a negative correlation between AMF colonization and tuber phosphorus percentage (Table 7), which is consistent with the other mentioned findings.

Photosynthetic capacity and maximum total dry weight

Based on the results of the analysis of variance, all traits related to the photosynthetic capacity (maximum LAI, chlorophylls a and b, transpiration rate, stomatal and mesophyll conductances, substomatal CO_2 concentration and net photosynthesis) and maximum total dry weight of potatoes were influenced by the effects of irrigation interval and biofertilizer, and some were also affected by the year of the study. The two-way interaction of biofertilizer × irrigation interval was significant for all traits except for chlorophyll a, b and transpiration rate (Table 4).

The highest maximum total dry matter, stomatal conductance, mesophyll conductance and net photosynthesis were observed using RF in irrigation after 70 mm of evaporation. For the maximum LAI, the application of FM in irrigation after 70 mm of evaporation resulted in the highest amount, however, at other levels of moisture stress, no significant difference between FM and RF was observed in terms of maximum LAI (Table 6). The

Table 4. Analysis of variance (mean squares) related to measured traits during two growing years (2019–2020)

S.O.V.	DF	Colonization	Tuber phosphorus	Leaf area index (max)	Total dry weight (max)	Chlorophyll a	Chlorophyll b	Transpiration rate	Stomatal conductance	Mesophyll conductance	Substomatal CO_2 concentration	Net photosynthetic rate	Tuber yield	Water productivity
Y	1	3642**	0.04**	0.47^{ns}	2 490 976^{ns}	0.009^{ns}	0.39**	108**	0.02*	0.01**	1156^{ns}	701**	1 663 171**	0.27^{ns}
Repeat × Y	4	66.8	0.005	0.28	5 489 227	0.01	0.03	1.76	0.002	0.00005	425	3.41	73 613	0.4
I	3	2621**	0.83**	45.3 **	62 177 460**	3.81**	5.92**	37.8**	0.18*	0.016**	10 877**	346**	22 792 924**	13.1**
Y × I	3	41.2**	0.003^{ns}	0.13^{ns}	79 330^{ns}	0.004^{ns}	0.008^{ns}	0.006^{ns}	0.0004^{ns}	0.000004^{ns}	12.5^{ns}	2.05^{ns}	20 839^{ns}	3.2**
B	5	22 108**	0.03**	6.72 **	4 292 208**	0.29**	0.29**	1.76*	0.01*	0.0015**	1144**	31.4**	2 036 302**	12.5**
Y × B	5	72.5**	0.0005^{ns}	0.03^{ns}	7601^{ns}	0.009^{ns}	0.01^{ns}	0.06^{ns}	0.0003^{ns}	0.0000007^{ns}	3.43^{ns}	4^{ns}	2912^{ns}	1.04*
B × I	15	295**	0.05**	0.76 **	976 859**	0.009^{ns}	0.01^{ns}	0.03^{ns}	0.03*	0.00022**	75 324*	4.81**	356 209**	2.33**
B × I × Y	15	4.74^{ns}	0.0003^{ns}	0.10^{ns}	2770^{ns}	0.004^{ns}	0.009^{ns}	0.029^{ns}	0.0005^{ns}	0.0000001^{ns}	5.00^{ns}	1.05^{ns}	2406^{ns}	0.37^{ns}
Error	92	8.91	0.002	0.18	335 727	0.007	0.01	0.03	0.001	0.00007	258	1.82	92 889	0.34
CV (%)	–	7.70	11.7	10.9	11.1	6.52	7.81	9.80	9.2	8.37	7.13	6.01	9.18	8.55

S.O.V., sources of variation; DF, degrees of freedom; CO_2, carbon dioxide; Y, year; I, irrigation; B, biofertilizers; ns, * and ** are non-significant, significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

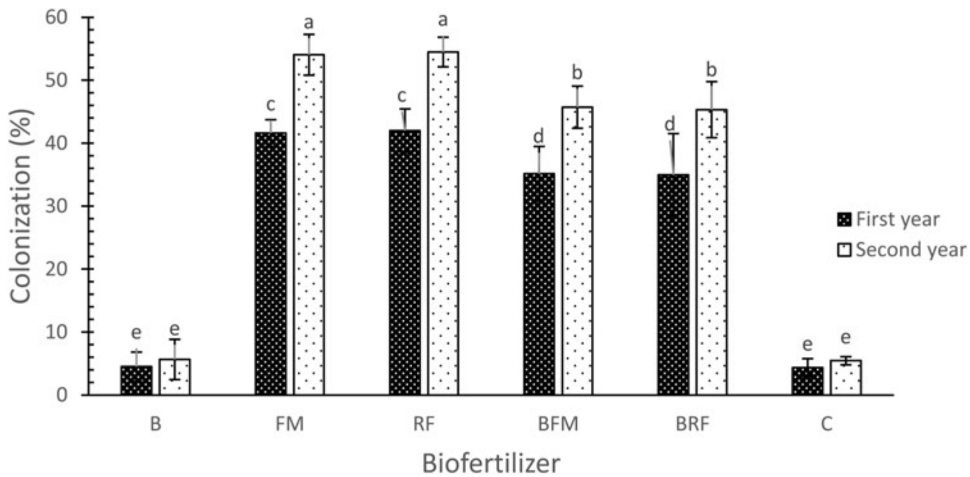

Figure 1. Means comparison for biofertilizer × year interaction on the root mycorrhizal colonization percentage. Error bars represent standard error. Significant differences between treatments are indicated by different letters ($\alpha = 0.05$).) FM, *Funneliformis mosseae*; RF, *Rhizoglomus fasciculatum*; B, phosphate-solubilizing bacteria; BFM, B + FM; BRF, B + RF combination; C, control).

lowest concentrations of substomatal CO_2 were also observed with the use of RF under irrigation conditions after 70 mm of evaporation, although it was statistically comparable to the other biofertilizer treatments (Table 6). In this study, the highest amount of chlorophyll a was obtained with the application of RF, and chlorophyll b was obtained with the application of both mycorrhizae. Additionally, chlorophyll b was 9.6% higher in the second year. Also both stomatal and mesophyll conductances were higher in the second year (Table 8). Transpiration rate showed a continuous decrease with increasing intensity of moisture stress, and its amount was 11.9% higher in the second year. The separate application of each of the biofertilizers was able to maintain transpiration rates high, but simultaneous use of mycorrhizae with PSB reduced transpiration rates (Table 8).

Based on the regression relationships obtained between the measured traits and the intensity of moisture stress (Table 5), it was determined that despite having a steeper decline slope against increasing moisture stress, mycorrhiza RF demonstrates higher values of traits, followed by mycorrhiza FM showing such a characteristic. However, concerning the total dry weight, the application of RF + PSB also exhibited similar results to RF (Table 5). Regarding the substomatal CO_2 concentration, which exhibits an opposite trend in its change slope compared to other traits concerning moisture stress intensity, the application of both types of mycorrhizae, especially RF, managed to create the lowest amount of CO_2 concentration in the stomatal cavity at different levels of moisture stress. However, at higher levels of moisture stress intensity, the combination of RF + PSB was also beneficial (Table 5). Although the application of PSB + both types of mycorrhizae did not result in significant benefits compared to the control treatment (without biofertilizer), the use of both types of mycorrhizae led to a significant increase in net photosynthesis at all levels of moisture stress (Table 6). However, the rate of decrease in net photosynthesis with increasing moisture stress intensity was higher compared to other biofertilizer treatments (Table 5).

In the correlation analysis between traits, it was also evident that except for the correlation of substomatal CO_2 concentration with all traits and the phosphorus percentage of tubers with all traits, which were negative, the rest of the traits generally showed positive correlations with each other (Table 7).

Tuber yield and water productivity

According to the results of the analysis of variance (Table 4), tuber yield was influenced by the main effects of year, irrigation interval, biofertilizer and the interaction of biofertilizer × irrigation interval. Meanwhile, water productivity, in addition to the main effects of irrigation interval and biofertilizer, and their two-way interaction, was under the influence of the two-way effects of year × irrigation interval and year × biofertilizer.

The tuber yield in the second year was 6.7% higher compared to the first year, and it decreased with an increase in the intensity of moisture stress (Table 8). In the second year of the research, when tuber yield is higher, stomatal conductance, mesophyll conductance, transpiration rate and net photosynthesis have also been higher (Table 8). Considering the reduction in growth indices such as LAI and photosynthetic parameters, especially net photosynthesis, under the influence of moisture stress, it is observed that tuber yield has also decreased with increasing intensity of moisture stress (Table 6). The application of biofertilizers, especially mycorrhizae, under all moisture stress levels has led to an increase in LAI, total dry matter and photosynthetic parameters (except for substomatal CO_2 concentration); therefore, the use of these biofertilizers has resulted in an improvement in tuber yield (Table 6). However, the combination of PSB and FM had less effect than other biofertilizer treatments. Under severe moisture stress conditions (irrigation after 130 mm of evaporation), only the separate use of biofertilizers was beneficial. The separate use of PSB and mycorrhizal species increased tuber yield by 48.4 and 61.3%, respectively (Table 6), meanwhile, the slope of decrease for all biofertilizer treatments in response to moisture stress was nearly similar (Table 5).

The means comparison results for the year × irrigation interval interaction showed that with an increase in moisture stress intensity, water productivity decreased in both cropping years (Fig. 2). However, the water productivity in the second cropping year was significantly higher than the first year for irrigation after 70 and 110 mm of evaporation. Nonetheless, the slope of decreasing water productivity against moisture stress intensity was higher in the second year (Fig. 2). Regarding the interaction of year × biofertilizer, it was observed that the use of both mycorrhiza species of FM and RF resulted in the highest water productivity in

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Table 5. Linear regressions between measured traits (y) and irrigation intervals (irrigation after x mm of cumulative evaporation)

Fertilizer treatments	Colonization (%)	Tuber Phosphorus	Leaf area index (max)	Total dry weight (max) (g/m^2)	Stomatal conductance (mol CO_2/m^2/s)	Mesophyll conductance (mmol CO_2/m^2/s)	Substomatal CO_2 (µmol/mol)	Net photosynthetic rate (µmol CO_2/m^2/s)	Tuber yield (g/m^2)	Water productivity (kg/m^3)
B	–	y = 0.0055x – 0.1878	y = −0.041x + 8.15	y = −57.62x + 11 174	y = −0.0027x + 0.627	y = −0.00084x + 0.187	y = 0.69x + 150	y = −0.10x + 33.8	y = −27x + 6063	y = −0.016x + 8.9
R^2	–	0.98	0.97	0.89	0.99	0.98	0.98	0.98	0.99	0.83
SE_b, SE_a	–	0.019, 0.00019	0.51, 0.005	1464 14.3	0.019, 0.00019	0.0074, 7.23	6.17, 0.06	0.95, 0.0093	167, 1.62	0.52, 0.0051
BRF	y = −0.337x + 74.2	y = 0.0068x – 0.3108	y = −0.037x + 7.44	y = −34.2x + 8526	y = −0.0026x + 0.5992	y = −0.0006x + 0.16	Y = 0. 69x + 170	y = −0.11x + 32.6	y = −29.2x + 6355	y = −0.0092x + 7.57
R^2	0.97	0.96	0.93	0.97	0.97	0.99	0.95	0.98	0.97	0.83
SE_b, SE_a	4.22, 0.041	0.044, 0.00043	0.72, 0.007	431, 4.20	0.027, 0.00027	0.0034, 3.33	8.91, 0.08	0.99, 0.0096	383, 3.73	0.29, 0.0029
BFM	y = −0.305x + 70.7	y = 0.0058x – 0.0852	y = −0.041x + 7.82	y = −60.3x + 11 255	y = −0.0027x + 0.6083	y = −0.0007x + 0.16	y = 0.71x + 154	y = −0.13x + 31.3	y = −27.8x + 5860.2	y = −0.006x + 9.41
R^2	0.95	0.98	0.98	0.99	0.99	0.99	0.99	0.99	0.99	0.85
SE_b, SE_a	4.75, 0.046	0.014, 0.00014	0.41, 0.004	3433.34	0.012, 0.00011	0.0007, 6.99	5.40, 0.74	0.057, 0.00056	192, 1.87	0.78, 0.0076
C	–	y = 0.0055x – 0.165	y = −0.041x + 7.43	y = −57.8x + 10 220	y = −0.0026x + 0.5817	y = −0.0006x + 0.15	y = 0.74x + 164	y = −0.15x + 31.0	y = −31.8x + 5700	y = −0.031x + 8.88
R^2	–	0.96	0.96	0.99	0.99	0.99	0.97	0.98	0.96	0.91
SE_b, SE_a	–	0.0072, 0.000070	0.55, 0.006	255.8, 2.49	0.014, 0.00014	0.0037, 3.62	8.19, 0.71	0.75, 0.0073	380, 3.70	0.69, 0.0067
RF	y = −0.460x + 94.3	y = 0.0047x – 0.0852	y = −0.034x + 7.9	y = −48.32x + 10 511	y = −0.0035x + 0.74	y = −0.001x + 0.22	y = 0.56x + 148	y = −0.09x + 39.9	y = −24.31x + 6670	y = −0.0016x + 7.67
R^2	0.97	0.99	0.95	0.93	0.96	0.90	0.97	0.90	0.99	0.92
SE_b, SE_a	4.81, 0.023	0.012, 0.00011	0.55, 0.005	769, 7.50	0.044, 0.0004	0.026, 0.00025	8.65, 0.084	3.71, 0.036	126, 1.22	0.65, 0.0064
FM	y = −0.397x + 87.6	y = 0.0064x – 0.1865	y = −0.0423x + 8.62	y = −44.534x + 9819	y = −0.0024x + 0.61	y = −0.001x + 0.2044	y = 0.55x + 157	y = −0.09x + 37.6	y = −25.4x + 6132	y = −0.0045x + 8.24
R^2	0.99	0.97	0.98	0.83	0.99	0.94	0.98	0.94	0.99	0.22
SE_b, SE_a	2.48, 0.02	0.027, 0.00027	0.36, 0.003	9818, 13.7	0.0072, 7.08	12.2, 0.0016	5.30, 0.051	2.50, 0.024	23.7, 0.23	0.61, 0.0059

CO_2, carbon dioxide; FM, *Funneliformis mosseae*; RF, *Rhizoglomus fasciculatum*; B, phosphate-solubilizing bacteria; BFM, B + FM; BRF, B + RF; C, control; R^2, coefficient of determination; SE_b, standard error of the slope of the line; SE_a, standard error of the intercept.

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Table 6. Means comparison for biofertilizer × irrigation interval interaction during two growing years (2019–2020)

Irrigation (mm evaporation)		Colonization (%)	Tuber phosphorus (%)	Leaf area index (max)	Total dry weight (max) (g/m^2)	Stomatal conductance (mol CO_2/m^2/s)	Mesophyll conductance (mmol CO_2/m^2/s)	Substomatal CO_2 (µmo/mol)	Net photosynthetic rate (µmol CO_2/m^2/s)	Tuber yield (g/m^2)	Water productivity (kg/m^3)
70	B	7.1i	0.23klm	5.24bc	6983a	0.44bc	0.13c	198jk	25.8b	4248a	7.64ab
	BRF	48.3d	0.25klm	4.56de	6151bc	0.43bcd	0.12d	212h–k	25.4bc	4057a	6.83c–g
	BFM	50.6cd	0.20m	4.87cd	6968.a	0.42bcd	0.11de	208h–k	24.4bcd	3916b	7.41ab
	C	6.43i	0.21lm	4.35ef	6088bcd	0.41de	0.11ef	217ghi	23.9cde	3525de	6.47f–i
	RF	60.8a	0.26kl	5.57b	7345a	0.51a	0.15a	194k	30.0a	4677a	7.42ab
	FM	59.5a	0.27k	5.75a	6293b	0.44b	0.14b	200ijk	28.6a	4438a	7.81a
90	B	6.21i	0.33ij	4.64de	5845b–e	0.37efg	0.107efg	217ghi	23.4d–h	3724bcd	7.48a–g
	BRF	43.6e	0.33i	4.4ef	5536c–f	0.35fg	0.105fgh	218ghi	22.7e–i	3518bcd	6.91c–g
	BFM	44.8e	0.27k	4.27ef	5836b–e	0.37efg	0.11fgh	220fgh	22.4e–i	3473cd	7.17a–g
	C	6.13i	0.27jk	3.97f	5106fgh	0.35gh	0.09ghi	225d–h	22.3f–i	3251ef	6.27ghi
	RF	55.3b	0.34hi	4.57de	5766b–f	0.41cde	0.11def	215hij	23.8b–f	4029ab	7.58a–d
	FM	52.5c	0.37ghi	4.63de	6171bc	0.39def	0.11def	216g–j	23.7d–g	3933b	7.88a
110	B	5.43i	0.39gh	3.41g	5587c–f	0.31hi	0.09hij	226c–h	21.8ijk	3098fg	7.39abc
	BRF	39.3f	0.48ef	3.24gh	4546hij	0.31hi	0.09ijk	236b–f	21.5i–l	3043fg	6.54e–i
	BFM	34.9g	0.36ghi	3.1gh	4783ghi	0.31ij	0.08jkl	235b–g	20.5j–m	2963de	6.88b–g
	C	5.21i	0.41g	2.78hi	3921jkl	0.31ij	0.08klm	242a–d	20.4klm	2496i	5.64i
	RF	42.5e	0.47f	4.33ef	5338efg	0.35gh	0.09ghi	224e–h	22.2ghi	3559de	7.8ab
	FM	45.3e	0.52def	4.07f	5424d–g	0.35gh	0.09hi	225d–h	22.0hij	3455fgh	8.04a
130	B	4.34ij	0.57bcd	2.92ghi	3228mn	0.27jkl	0.07mno	241a–e	18.8no	2712hi	6.63d–h
	BRF	29.4h	0.60abc	2.43ij	4203ijk	0.27jkl	0.08lmn	244abc	18.8no	2098jk	6.34e–i
	BFM	31.4h	0.62ab	2.5i	3296lm	0.26kl	0.07no	253ab	18.6no	2286jk	5.75i
	C	4.79ij	0.53de	1.97j	2626.5n	0.24l	0.06o	258.8a	17.87o	1827k	4.58j
	RF	34.37g	0.55cd	3.33g	4266ij	0.29ijk	0.08klm	237.8b–f	19.95lmn	2919ghi	7.24a–f
	FM	35.08g	0.65a	3.12gh	3573.2klm	0.31ij	0.08klm	238.5b–e	19.81mn	2977ghi	7.45ab

CO_2, carbon dioxide; FM, *Funneliformis mosseae*; RF, *Rhizoglomus fasciculatum*; B, phosphate-solubilizing bacteria; BFM, B + FM; BRF, B + RF; C, control.
In each trait significant differences between treatments are indicated by different letters ($\alpha = 0.05$).

Table 7. Pearson correlation coefficients between measured traits (1: colonization, 2: maximum of leaf area index, 3: total dry weight, 4: transpiration rate, 5: stomatal conductance, 6: mesophyll conductance, 7: substomatal CO_2, 8: net photosynthetic rate, 9: tuber yield, 10: water productivity, 11: chlorophyll a, 12: chlorophyll b, 13: tuber phosphorus)

No	1	2	3	4	5	6	7	8	9	10	11	12	13
1	1												
2	0.39*	1											
3	0.37**	0.76**	1										
4	0.09^{ns}	0.57**	0.36**	1									
5	0.34**	0.81**	0.69**	0.66**	1								
6	0.42**	0.79**	0.82**	0.30**	0.72**	1							
7	−0.26**	−0.69**	−0.61**	−0.57**	−0.67**	−0.73**	1						
8	0.41**	0.69**	0.78**	0.09^{ns}	0.59**	0.94**	−0.48**	1					
9	0.39**	0.80**	0.88**	0.50**	0.78**	0.81**	−0.67**	0.72**	1				
10	0.45**	0.56**	0.63**	0.35**	0.54*	0.54**	−0.49*	0.46**	0.78**	1			
11	0.39**	0.86**	0.82**	0.54**	0.82**	0.84**	−0.73**	0.74**	0.87**	0.60**	1		
12	0.37**	0.86**	0.80**	0.58**	0.84**	0.82**	−0.70**	0.72**	0.83**	0.54**	0.90**	1	
13	−0.08**	−0.67**	−0.71**	−0.54**	−0.70**	−0.64**	0.56**	−0.57**	−0.73**	−0.33**	−0.76*	−0.76**	1

ns, * and ** are non-significant, significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

both years. In the first cropping year, the use of PSB alone along with both mycorrhiza species increased water productivity (Fig. 3). At all levels of moisture stress, the application of both mycorrhiza species and PSB alone helped maintain high water productivity. Furthermore, the combination of PSB with mycorrhiza, especially FM, showed good performance at low intensities of moisture stress (Table 6). In the analysis of the regression equations of water productivity against moisture stress, it was observed that the highest decreasing slope was obtained in the control treatment (without biofertilizer), and the lowest in the use of RF. However, the use of FM and the combination of PSB with both species of mycorrhiza significantly improved water productivity (Table 5).

Water productivity, like tuber yield, exhibited a negative correlation with tuber phosphorus and substomatal CO_2 concentration. However, they showed a positive correlation with other measured traits (Table 7).

Discussion

The results from this study indicate that in treatments where mycorrhiza was applied, a satisfactory symbiosis was established between potato roots and both mycorrhizal species (*R. fasciculatum* and *F. mosseae*). However, this symbiosis was reduced in the presence of PSB, likely due to the high concentration of soil phosphorus in the rhizosphere area, which may lead to the decrease of AMF (Smith and Read, 2008). High levels of phosphorus inhibit the secretion of strigolactones, which are plant hormones that stimulate mycorrhizal growth (Balzergue *et al*., 2013) and reduce the development of arbuscules (Smith and Read, 2008; Bonneau *et al*., 2013). Under conditions of direct P absorption from the soil, plants may reduce mycorrhizal colonization to avoid carbon expenditure (Nagy *et al*., 2009), which can be up to 20% of photosynthetic carbon (Bago *et al*., 2000). The observed decrease in mycorrhizal hyphal growth in the presence of PSB may be due to competition for growth resources or a suppressive effect of PSB on mycorrhizae (Leigh *et al*., 2011). However, some studies have reported that PSB can improve AMF hyphal growth under conditions of phosphate fertilizer application (Zhang *et al*., 2016) and use AMF hyphae to colonize the rhizosphere and make better use of plant exudates (Ordoñez *et al*., 2016). Although the presence of PSB in the current study led to a decrease in mycorrhizal colonization, it also reduced the rate of colonization decrease with moisture stress (Table 5). This may be due to PSB's ability to increase root exudates (James *et al*., 2002), which could have helped reduce the rate of mycorrhizal colonization at higher levels of moisture stress. Additionally, PSB can increase plant tolerance to biotic and abiotic stresses (Rossi *et al*., 2021; Kim *et al*., 2022). Jarosław *et al*. (2020) reported the effect of cropping year on tuber yield, which is consistent with the results of the present study (Table 8). This may be the reason for the cooler second year of research (Table 2). In an experiment conducted by Batool *et al*. (2020), it was found that the tuber yield of potato increased with different treatments of PSB compared to the control treatment under normal and water stress conditions. PSB can produce plant hormones such as cytokinin, auxin and gibberellin (Luziatelli *et al*., 2021), which can enhance plant growth and yield. Additionally, AMF symbiosis is known to positively impact biochemical and physiological processes, including protection against oxidative damage, improved water productivity, increased shoot weight, enhanced gas exchange rate and improved osmotic regulation (Chen *et al*.,

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Table 8. Means comparison for main effects of year, irrigation interval and biofertilizer treatments on potato photosynthetic indices

Treatments	Substomatal CO_2 (μmol/mol)	Chlorophyll a (mg/g FW)	Chlorophyll b (mg/g FW)	Transpiration rate (mmol $H_2O/m^2/s$)	Stomatal conductance (mol $CO_2/m^2/s$)	Net photosynthetic rate (μmol $CO_2/m^2/s$)	Mesophyll conductance (mmol $CO_2/m^2/s$)	Tuber yield (g/m^2)	Water productivity (kg/m^3)
First year	222^{a}	1.34^{a}	0.52^{b}	6.11^{b}	0.34^{b}	20.2^{b}	0.092^{b}	3211^{b}	6.83^{a}
Second year	228^{a}	1.39^{a}	0.57^{a}	6.84^{a}	0.36^{a}	24.7^{a}	0.109^{a}	3425^{a}	6.92^{a}
Irrigation interval (mm cumulative evaporation)									
70	205^{d}	1.74^{a}	0.76^{a}	7.21^{a}	0.44^{a}	26.4^{a}	0.129^{a}	4179^{a}	7.44^{a}
90	218^{c}	1.45^{b}	0.56^{b}	6.40^{b}	0.37^{b}	23.1^{b}	0.105^{b}	3637^{b}	7.19^{a}
110	231^{b}	1.31^{c}	0.49^{c}	5.36^{c}	0.32^{c}	21.4^{c}	0.092^{c}	3153^{c}	6.82^{b}
130	245^{a}	0.95^{d}	0.35^{d}	4.95^{d}	0.27^{d}	19.0^{d}	0.077^{d}	2303^{d}	6.05^{c}
Biofertilizer treatments									
B	219^{bc}	1.39^{b}	0.54^{b}	6.28^{a}	0.35^{b}	22.5^{b}	0.103^{b}	3455^{ab}	6.97^{b}
FM	220^{bc}	1.42^{b}	062^{a}	6.10^{a}	0.37^{a}	24.0^{a}	0.108^{a}	3464^{ab}	7.47^{a}
RF	218^{c}	1.51^{a}	0.62^{a}	6.09^{a}	0.39^{a}	23.5^{a}	0.112^{a}	3617^{a}	7.71^{a}
BFM	229^{ab}	1.31^{c}	0.52^{b}	5.93^{b}	0.34^{b}	21.5^{cd}	0.095^{cd}	3225^{bc}	6.72^{b}
BRF	227^{ab}	1.34^{c}	0.53^{b}	6.0^{b}	0.34^{b}	22.1^{b}	0.098^{bc}	3271^{c}	6.73^{b}
C	236^{a}	1.18^{d}	0.47^{c}	5.48^{c}	0.32^{c}	21.1^{d}	0.090^{d}	2777^{d}	5.65^{c}

CO_2, carbon dioxide; FM, *Funneliformis mosseae*; RF, *Rhizoglomus fasciculatum*; B, phosphate-solubilizing bacteria; BFM, B + FM; BRF, B + RF; C, control.
In each trait significant differences between treatments are indicated by different letters ($\alpha = 0.05$).

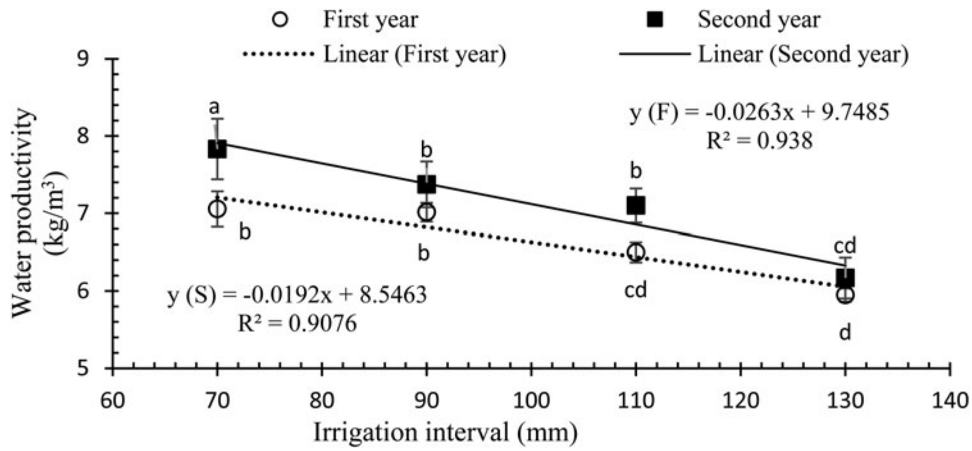

Figure 2. Means comparison for year × irrigation interval interaction on water productivity. Error bars represent standard error Significant differences between treatments are indicated by different letters.

2017). The results of this study on photosynthetic parameters and tuber yield indicate that inoculation with mycorrhizal species can promote the growth of potatoes. Mycorrhizal symbiosis can alter the physiology and environment of the host plant, leading to increased nutrient uptake, particularly under conditions of low soil absorbable phosphorus, which can also have a positive effect on the microbial population of the soil (Elliott *et al*., 2021).

Khosravifar *et al*. (2020) reported that with an increase in the intensity of moisture stress, the phosphorus concentration in the tubers increased. This outcome aligns with the observations in current study. Similar results were documented by Wegener *et al*. (2017), who noted a significant phosphorus content increase in potato tubers under moisture stress conditions. The elevated phosphorus concentration in tubers under intensified moisture stress is attributed to a more substantial decrease in tuber yield compared to the reduction in phosphorus absorption. The application of biofertilizers, especially FM, increased the phosphorus concentration in tubers. As a result, the highest phosphorus concentration under severe moisture stress was achieved with the application of FM (Table 6). In the experiment conducted by Ghobadi *et al*. (2020), mycorrhizal inoculation exhibited an augmentation in phosphorus levels in the shoot, root and tuber of

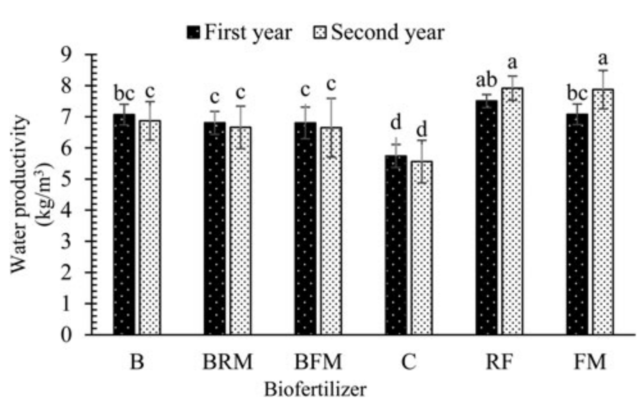

Figure 3. Means comparison for year × biofertilizer interaction on potato water productivity. Error bars represent standard error. Significant differences between treatments are indicated by different letters. (FM, *Funneliformis mosseae*; RF, *Rhizoglomus fasciculatum*; B, phosphate-solubilizing bacteria; BFM, B + FM; BRF, B + RF; C, control).

potato plants subjected to phosphorus deficiency stress treatment. The improvement of root development by mycorrhiza has been reported as a significant factor in enhancing phosphorus absorption (Mai *et al*., 2018).

It is evident that potato inoculation with RF has led to a higher chlorophyll content compared to FM, while the impact of FM has been comparable to that of PSB (Table 8). The superiority of RF may be attributed to the distinct behaviour of mycorrhizal fungi in symbiosis with plants (Leventis *et al*., 2021). In the current study, despite the similarity in the colonization percentage of both mycorrhizal species, in the irrigation treatment after 90 mm of evaporation, the colonization percentage of RF is significantly higher than FM (Table 8). The decline in chlorophyll a levels under the influence of moisture stress is linked to an elevation in reactive oxygen species (ROS) within the cells. These ROS induce peroxidation, resulting in the degradation of chlorophyll pigment (Sadeghipour and Aghaei, 2012). The findings of Batool *et al*. (2020) revealed that moisture stress leads to a decrease in the concentration of chlorophyll b in potato leaves. Similarly, in an experiment conducted by Ghorbanli *et al*. (2013), it was reported that leaf chlorophyll a and b in tomato leaves were significantly reduced under moisture stress conditions. Rossi *et al*. (2021) reported that plants treated with plant growth-promoting bacteria (PGPB) exhibited elevated antioxidant activity under abiotic stress conditions. In the present study, the application of PSB, which is a type of PGPB, also led to an increase in chlorophyll a and b which may be a result of the improved antioxidant capacity of the potato plants. Enhanced plant nutrition through mycorrhizal inoculation, specifically improved absorption of nutrients like phosphorus, iron and magnesium, can serve as another reason for the increased content of leaf chlorophyll. The findings of Han and Lee (2005) demonstrated that nutrients, such as phosphorus, play a crucial role in sustaining carbon dioxide fixation, photosynthesis and protecting chloroplasts under stress conditions.

These findings underscore the ecological significance of AMF in both natural and agricultural ecosystems. Furthermore, the mycorrhizal hyphae network can interconnect the roots of different plant species, facilitating the transfer of nutrients, particularly nitrogen and phosphorus, from donor to recipient plants (Simard, 2018). In a study on two sweet potato varieties, the use of mycorrhiza was found to enhance growth and increase marketable root

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storage by 18.3% (Sakha and Jefwa, 2019). Mycorrhizal symbiosis with plants can affect stomatal conductance through abscisic acid biosynthesis, leading to increased assimilate flow towards plant roots (Hajiboland *et al.*, 2010). The increased dry weight observed in mycorrhizal plants may be attributed to improvements in leaf chlorophyll content and enhanced absorption of nutrients such as nitrogen, iron, copper, zinc and manganese (Chen *et al.*, 2017). Another significant outcome of this study was the high correlation between the percentage of colonization and other traits, except for substomatal CO_2 concentration (Table 7).

Moisture stress can cause a reduction in photosynthetic activity in plants (Batool *et al.*, 2020). The decrease in photosynthesis is primarily due to the reduction in CO_2 absorption, which is caused by decreased stomatal and mesophilic conductances (Retuerto *et al.*, 2006; Marcińska *et al.*, 2013). In the present study, the greater reduction in the gradient of stomatal and mesophyll conductances under moisture stress in the mycorrhizal treatment alone suggests better management of stomatal movement, leading to a reduction in water loss and an increase in water productivity (Table 8). The higher water productivity observed in the second year of the study (Fig. 2) may be attributed to the cooler weather conditions. Dadrasi *et al.* (2022*b*) have also reported the coolness of the growth environment as a factor in improving potato water productivity. Mycorrhizal symbiosis has been reported to improve photosynthesis through morphological changes, such as increasing the number and area of leaves and enhancing nutrient uptake (Begum *et al.*, 2019). In an experiment conducted by Batool *et al.* (2020), potatoes treated with growth-promoting rhizobacteria had a greater leaf area compared to control plants, both under drought stress and non-stress conditions. This may be due to the increased availability of nutrients, particularly phosphorus, and the production of hormone-like substances (Vacheron *et al.*, 2013). Similarly, a study on bean plants reported a significant increase in photosynthesis with rhizobial inoculation, by 140% for the glasshouse experiment and by 81% in the field experiment, compared to the control (Bambara and Ndakidemi, 2009).

Overall, the present study suggests that mycorrhizal species, particularly under moisture stress conditions, can mitigate the adverse effects of stress and improve growth conditions and photosynthetic traits in potatoes. These findings have implications for the development of sustainable agricultural practices aimed at improving crop productivity and resilience in the face of changing environmental conditions.

Conclusion

In conclusion, the results from this study demonstrate that irrigation interval and biofertilizer treatments have a significant impact on the physiological and photosynthetic traits as well as the tuber yield of potato. As the intensity of moisture stress increased, most measured traits decreased, except for substomatal CO_2 concentration. However, the use of biofertilizers, including *F. mosseae*, *R. fasciculatum* and PSB alone, improved potato growth and tuber yield. The application of AMF and PSB enhanced stomatal and mesophilic conductance, increased net photosynthesis and improved water productivity. The efficiency of two species of AMF alone was found to be better than the combination of mycorrhiza with PSB.

Data. The data that support the findings of this study are available on request from the corresponding author.

Author contributions. A. Nemati and M. A. Aboutalebian planned and designed the research, analysed data through consultation with M. Chaichi. All authors reviewed and edited the final manuscript. Supervision of the research was done by M. A. Aboutalebian.

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Ethical standards and consent to participate. This study did not involve any human participants or animals.

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