

EFFECTS OF BACTERIAL INOCULANTS AND IRRIGATION REGIMES ON YIELD, MYCORRHIZAL COLONISATION, AND PHOTOSYNTHETIC EFFICIENCY IN STRAWBERRY CULTIVARS

Krzysztof Górnik¹✉, Lidia Sas-Paszt¹, Edyta Derkowska¹,
Walid F.A. Mosa², Paweł Trzcíński¹, Sławomir Głuszek¹

¹ Department of Microbiology and Rhizosphere, The National Institute of Horticultural Research, Konstytucji 3 Maja 1/3, 96-100 Skierniewice, Poland

² Plant Production Department (Horticulture-Pomology), Faculty of Agriculture, Saba Basha, Alexandria University, Alexandria 21531, Egypt

ABSTRACT

Strawberries (*Fragaria* × *ananassa*) are a globally significant fruit crop with high nutritional and economic value. However, their shallow roots and high water demands make them vulnerable to water stress. The effects of microbial inoculants and irrigation regimes on the yield, root colonisation by arbuscular mycorrhizal fungi (AMF), and photosynthetic efficiency of strawberry cultivars Rumba and Honeoye were investigated. Field and pot experiments were conducted, where plants were subjected to 100% and 50% water supply conditions. The application of Inoculum 1 (C09EX – *Pseudomonas* sp., Ps 150AB *Pseudomonas* sp.) and Inoculum 2 (JAFGU – *Lysobacter* sp.) were applied to evaluate their potential to enhance plant growth and resilience under these conditions.

A full irrigation regime (100% water supply) significantly increased fruit yield per plant in both cultivars compared to a reduced irrigation regime (50% water supply). Both inoculants positively affected yield, with Inoculum 1 showing the best results under full irrigation and Inoculum 2 under reduced irrigation. Mycorrhizal colonisation of roots was significantly improved by both inoculants, with the highest colonisation levels observed in plants treated with Inoculum 2. Photosynthetic efficiency parameters, such as the maximum quantum yield of PSII (F_v/F_m) and quantum efficiency of photochemical reaction in PSII (Φ_{PSII}), declined under reduced irrigation, particularly in Honeoye, but microbial inocula mitigated these effects and enhanced performance under both regimes.

These findings suggest that microbial inoculants can alleviate the adverse effects of water stress on strawberry plants, enhancing yield and physiological performance. Future research should explore the underlying mechanisms of these interactions and evaluate the long-term benefits of microbial inocula in different environmental conditions.

Keywords: bacterial inoculants, mycorrhiza, photosynthetic efficiency, irrigation regimes

INTRODUCTION

Strawberries are one of the most popular berry-like fruits and can be widely produced in almost all regions of the world due to their delicious taste and nutrition-

al value. The strawberry (*Fragaria* × *ananassa*) is a result of crossbreeding between two wild strawberries, *Fragaria virginiana* and *Fragaria chiloensis*.

Although the parent species are native to the Americas, the hybrid we know today was developed in Europe using imported specimens [Morais et al. 2019].

Strawberries have a prominent position among the fruit-bearing plants in the world. Consumers prefer it because it is the first fruit to ripen in the spring when no other fruit is available, and it is one of the most profitable fruits due to its nutritional value and benefits for human health [Morais et al. 2019]. For this reason, fruits can find buyers at high prices until other fruits reach the market. The demand for marketing fresh strawberries is very high in the world market because strawberries are widely used either fresh or in processed foods, such as fruit juices, jams, jellies, ice creams, chocolates, pies, syrups, pastries, and many beverages [Sahana et al. 2020, Sharma et al. 2023, Azam et al. 2019]. According to Food and Agriculture Organization [FAO 2023] data, in 2022, world strawberry production was 10.2 million tons. While China ranks first with 4 million tons of production, the USA ranks second with 1.3 million tons, and Turkey ranks third with 728 thousand tons. Poland holds the eighth position in this ranking with 199 thousand tons. In terms of cultivation area, Poland ranks third with 31.3 thousand hectares [FAO 2023].

Several challenges occur in strawberry cultivation in Poland. Among the most significant are climatic constraints, such as drought, which adversely affect both plant growth and fruit quality. Additionally, the Polish climate is highly variable, with unpredictable winter and spring conditions. Late frosts can damage strawberry flowers and newly formed fruit, impacting yield and quality.

In light of these challenges, recent studies emphasize the potential of combining microbial inoculants with different irrigation regimes as a strategy to enhance strawberry physiology and productivity. Chioimento et al. [2024] demonstrated that combinations of mycorrhizal fungi (AMF), *Trichoderma harzianum*, and *Ascophyllum nodosum* improved strawberry fruit weight and synchrony under variable water regimes. Similarly, Haghshenas et al. [2024] showed that inoculated strawberry plants cultivated in nutrient-limited substrates exhibited increased root colonization and enhanced yield parameters.

The beneficial effects of microbial inoculants have also been documented in other horticultural crops.

In organic sweet pepper systems, AMF inoculation combined with drip irrigation led to improved soil microbial activity and plant health [Jamiołkowska et al. 2020]. Likewise, Chen et al. [2017] observed that cucumber seedlings inoculated with consortia of AMF exhibited superior photosynthetic performance, biomass accumulation, and phosphorus uptake.

Further support comes from a review by Shahrajabian et al. [2023], who compiled successful applications of microbial biostimulants across various horticultural crops, including tomato and pepper, highlighting their role in improving plant productivity and stress tolerance. In strawberries, Todeschini et al. [2018] reported that beneficial microbes enhanced fruit yield, nutritional value, and photosynthetic pigment composition. Moreover, Cecatto et al. [2016] linked increased AMF colonization with elevated levels of phytochemicals and enhanced antioxidant capacity in strawberry fruit.

The results obtained by Pérez-Moncada et al. [2024] provided additional field-based evidence that the integration of AMF and *Bacillus* spp. contributes to improved fruit development, chlorophyll biosynthesis, and plant tolerance to water stress in strawberry cultivation under semi-controlled conditions.

The application of endophytic bacteria in strawberry production has garnered interest. Mei et al. [2021] explored the potential of endophytic bacteria in improving strawberry growth and yield. Endophytes are bacteria that reside within plant tissues without causing harm, and their presence has been associated with enhanced plant growth, nutrient uptake, and disease resistance. These researchers demonstrated that certain endophytic bacteria positively influenced strawberry growth parameters and exhibited potential as biocontrol agents against *Botrytis cinerea*, a common fungal pathogen affecting strawberries.

Water deficit is a significant challenge in strawberry production, and researchers have investigated the potential of bacterial inoculants in mitigating its negative effects. Paliwoda et al. [2022] studied the effects of rhizosphere bacteria on strawberry plants under water deficit conditions. The results showed that certain bacterial strains enhanced plant growth, photosynthetic efficiency, and antioxidant enzyme activities, thus improving the ability of plants to withstand water stress.

Furthermore, the combined effects of bacterial inoculants with other agricultural practices have been investigated. Oregel-Zamudio et al. [2017] explored the impact of candelilla wax edible coatings combined with biocontrol bacteria on strawberry quality during shelf-life. Findings from the study indicated that the treatments improved the postharvest quality and extended the shelf-life of strawberries by reducing decay and maintaining fruit firmness.

Understanding the interactions between bacterial inoculants and strawberry plants is crucial for developing sustainable agricultural practices. Further research is needed to unravel the specific mechanisms by which bacterial inoculants promote strawberry growth and to optimise their application methods. By exploiting the potential of bacterial inoculants, strawberry growers can enhance crop productivity, reduce reliance on chemical inputs, and contribute to more sustainable and environmentally friendly strawberry cultivation.

The objective of the current study was to evaluate the effects of bacterial inoculants on the yield, mycorrhizal colonisation, and photosynthetic efficiency of strawberry plants in field and pot cultivation under different irrigation regimes. By examining the results of studies conducted in the field, valuable insights can be gained into the mechanisms underlying the positive effects of bacterial inoculation and their potential applications in strawberry production.

MATERIALS AND METHODS

Field and pot experiments on strawberry plants of Rumba and Honeoye cultivars were carried out in 2021, at the National Institute of Horticultural Research in Skierniewice in Ecological Experimental Field (Central Poland, latitude 51.914210 N, longitude 20.111524 E, 128 meters above sea level).

For the field experiment, due to ecological cultivation and the elimination of chemical weed control methods, the plants were planted on agrotexile (50 cm wide in experimental rows) and irrigated using a drip system. The experiment was conducted in four replicates, with each replicate including 75 plants. Strawberry plants were purchased from a licensed nursery and were planted in the field during the third decade of October 2018.

In the pot experiment, strawberry plants were planted in vases also during the third decade of October 2018 filled with podzolic soil, each 40 cm in diameter. Each vase was inserted in the soil of the Ecological Experimental Field and 25 cm from each other. The pot experiment was planned in seven replications (vases), each containing three plants.

In the first half of May of 2019, 2020, and 2021, a certified organic fertiliser, Bioilsa 6-5-13 (NPK), was applied as a soil application at a dose of 9 g/plant (350 kg/ha).

The experiment consisted of two blocks irrigated by drip technique; under one of them, the plants received the full dose of water (100% irrigated), and under the second block, the plants received irrigation with 50% water supply. The water requirements were adjusted according to the indications of tensiometers installed in the root zone. Irrigation was scheduled each morning at 07:00 h based on soil-water tension recorded by tensiometers in the open-field strawberry crop. When the tensiometer reading reached 30 cbar (≈ 30 kPa), the irrigation valve in the 100% block was opened fully, and in the 50% block it was opened to exactly half its maximum flow rate, thereby delivering 100 % and 50% of the target water supply, respectively. During the flowering and fruiting phases, each irrigation event lasted 30 minutes; in all other developmental stages, it lasted 20 minutes. This daily, valve-based adjustment maintained the intended water regimes under open-field conditions. Each block comprised the same three treatments. All treatments under each block were repeated four times.

- Control plants treated with organic fertiliser Bioilsa 6-5-13 (9 g/plant) as a soil application.
- Plants treated with Inoculum 1 of microorganisms with 9 g/plant of Bioilsa 6-5-13.
- Plants treated with Inoculum 2 with 9 g/plant of Bioilsa 6-5-13.

Bacterial strains used in inoculants

For the experiments, three non-rhizosphere strains of bacteria were selected and included in two different inocula.

I. Inoculum 1: strains:

- C10C09 – *Pseudomonas* sp. strain isolated from non-rhizosphere soil under an apple tree in Rowiska, Poland (Fig. 1),

- AF70AC – *Pseudomonas* sp., strain isolated from non-rhizosphere soil under an apple tree in the Pieprzowe Mountains, Poland (Fig. 2).

Pseudomonas strains exhibit plant growth-promoting potential through mechanisms such as siderophore production and calcium phosphate solubilisation. Additionally, these bacterial strains demonstrate antagonistic activity against *Verticillium*, *Fusarium*, *Botrytis*, and *Colletotrichum*.

- II. Inoculum 2: strain JAFGU – *Lysobacter* sp.; strain isolated from non-rhizosphere soil in a strawberry cultivation field, Skierniewice, Poland.

Lysobacter sp. bacterial strain exhibits antagonistic properties against *Verticillium*, *Fusarium*, *Botrytis*, and *Colletotrichum*.

The bacteria chosen for the study produced secondary metabolites toxic to *Verticillium*, *Fusarium*, *Botrytis* and *Colletotrichum*. Additionally, the AF70AC and C10C09 produced the siderophores and were able to dissolve calcium phosphate in *in vitro* conditions. The strains from inoculum 1 did not have antagonistic activity toward each other.

The composition of the medium per litre for culturing bacterial strains consisted of 0.25 g glucose, 0.3 g soy peptone, 1.7 g casein peptone, 0.5 g NaCl and 0.25 g K_2HPO_4 .

The bacteria were identified by sequencing the gene encoding the 16S rRNA subunit. The GeneMa-

trix Bacterial & Yeast Genomic DNA Purification Kit (EURx) was used to isolate DNA, and the 16S rRNA gene was amplified using the primer pair 27F/1492R [Lane 1991]. The obtained DNA sequences were compared to NCBI data using the BLAST tool (National Center for Biotechnology Information, https://blast.ncbi.nlm.nih.gov/Blast.cgi?PAGE_TYPE=Blast-Search).

All strains used in this study are preserved in a sterile solution consisting of glycerol (30%), peptone (0.5%), yeast extract (0.3%), and distilled water (69.2%) and stored at $-80^{\circ}C$ in SYMBIO-BANK microorganism collection maintained by the National Institute of Horticultural Research, Department of Microbiology and Rhizosphere, Skierniewice, Poland.

Microbial inoculants were applied in 2019, 2020 and 2021 to the soil under the plants in strawberry cultivation using tractor-mounted sprayers equipped with ‘dropleg’ lances. The mounting of the “dropleg” lances allows for the adjustment of their position to match the row spacing of the crops and their tilt from the vertical according to the plant size. In the strawberry plantation, TF10 nozzles were used at a pressure of 3.4 bar. In the pot experiment, the microbial inoculants were applied to the soil using a backpack sprayer.

The present experiment was conducted in 2021 following two consecutive annual applications of the microbial inoculants (2019–2020). Although positive effects of microbial inoculation can be detected already in

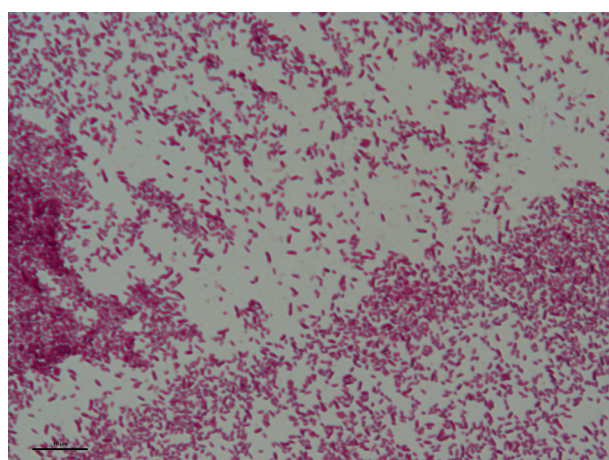


Fig. 1. Strain C10C09 – Gram staining. Material taken from a 24-hour culture (PCA medium)

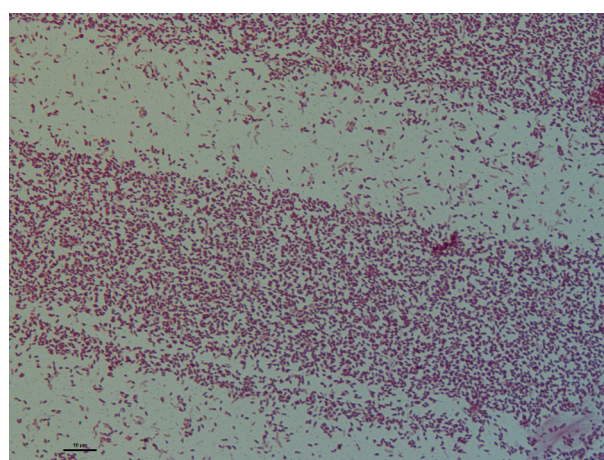


Fig. 2. Strain AF70AC – Gram staining. Material taken from a 48-hour culture (PCA medium)

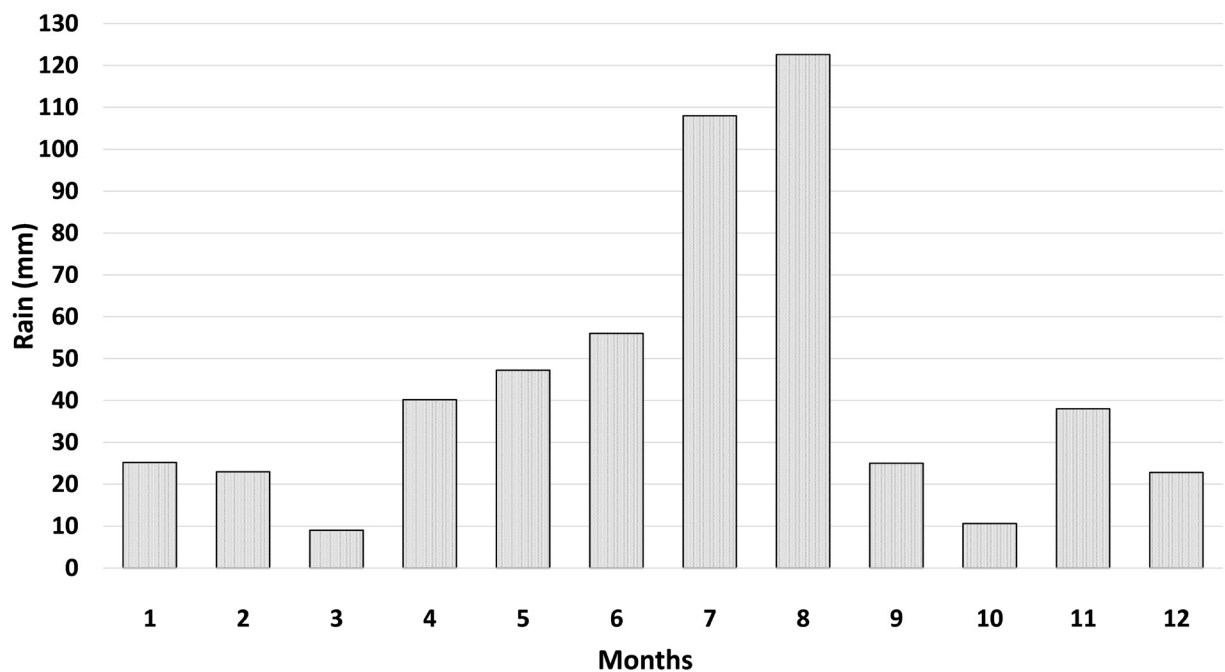


Fig. 3. Monthly precipitation at the experimental site (data from the weather station located in the Experimental Orchard)

the first year, both our investigations and international studies on orchard crops, including strawberry, demonstrate that the most pronounced and reproducible effects manifest in the second and third years of treatment.

The evaluation of strawberry plant roots for the presence of arbuscular mycorrhizal fungi growing under field and growth pot conditions

In September 2021, the root systems of Rumba and Honeoye strawberry plants were sampled from field and pot experiment (growth vases) to analyse the degree of mycorrhizal colonisation. Microbiological analyses of rhizosphere soil samples were performed on the same dates as fluorescence measurements (July and August 2021). The plants were treated with bacterial strains included in Inoculum 1 (plant growth-promoting potential) – C10C09, AF70AC (*Pseudomonas* spp.), and Inoculum 2 (antagonistic properties against pathogens) – JAFGU (*Lysobacter* sp.).

Segments of the root systems of strawberry (10 g from each replication) were collected from experiments and stained using the method developed at the Rhizosphere Laboratory of the National Institute of

Horticulture Research in Skierniewice [Derkowska et al. 2015]. Subsequently, microscopic preparations were made and analysed using a Nikon 50i microscope (objectives at magnifications: 20x, 40x, 60x, 100x), and photographic documentation of observed mycorrhizal structures was conducted. The assessment of root colonisation by arbuscular mycorrhizal fungi naturally present in the soil was performed using the Trouvelot method [1986]. Based on the obtained results, mycorrhizal frequency (F%), mycorrhizal intensity (m%, M%), and arbuscule abundance (a%, A%) were calculated using the MYCOCALC computer program, available on the website: <http://www2.dijon.inra.fr/mychintec/Mycocalc-prg/MYCOCALC.EXE>. The following parameters were observed: F – mycorrhizal frequency, M – relative mycorrhizal intensity, m – absolute mycorrhizal intensity, a – absolute abundance of arbuscular, and A – relative abundance of arbuscules.

Evaluation of strawberry fruits yield

The fruits of the strawberry varieties Rumba and Honeoye were harvested at full maturity twice a week for three weeks. The field experiment was planned in

four replications, each comprising 75 plants. The pot experiment was planned in seven replications (vases), each containing 3 plants.

Chlorophyll a fluorescence measurements

Chlorophyll fluorescence was determined during the 2021 growing season. Measurements were carried out in July and August 2021, corresponding to the fruit development and ripening stages (generative phase) of the crop. All fluorescence readings were taken in the morning between 08:30 and 11:00 h, immediately following scheduled irrigation events; thus, soil moisture was at or very near field capacity at the time of measurement.

Chlorophyll fluorescence was measured after fruit harvest during July–August 2021 in an open-field crop. Readings were taken in the morning (08:30–11:00 h) following irrigation, when soil moisture was at field capacity.

Chlorophyll fluorescence parameters were recorded on fully expanded leaves using a portable Pulse Amplitude Modulation (PAM) Chl fluorometer (FMS-1, Hansatech Instruments Ltd., King's Lynn, Norfolk, United Kingdom). The measurements were performed in 3 replications, each containing 10 plants. For measurements one leaf was taken for each plant. The measurements were taken at the same time of day. The fibre optic of the FMS-1 was positioned using the PPF/temperature leaf clip at a 60° angle from the upper surface of the leaf, and the distance between the leaf surface and the fiber optic was kept constant for all measurements. Before chlorophyll a fluorescence measurements, the leaves were dark-adapted for 30 min to obtain oxidoreduction equilibrium of PSII-PSI electron transport carriers.

The following parameters of chlorophyll fluorescence after dark adaptation were measured: F_0 – minimum fluorescence or initial fluorescence. This parameter indicates the excitation energy loss during its transmission from the energetic antennas to the PSII reaction centre, F_M – maximum fluorescence is attained when the dark-adapted sample is exposed to an intense saturating pulse of light. F_V – variable fluorescence; $F_V = F_M - F_0$. The value of this parameter depends on the maximum quantum yield of PSII.

- F_V/F_M – the maximum potential photochemical reaction efficiency in PS II,

- F_V/F_0 – the activity of PS II – the maximum efficiency of water decomposition on the donor side of PSII.

The following parameters of light-adapted leaves were measured:

- Φ_{PSII} – quantum yield of photosystem II photochemistry is directly associated with the electron transfer rate in PSII toward biochemical processes. This parameter measures the proportion of the light absorbed by PSII that is used in photochemistry and provides the rate of linear electron transport and so indicates overall photosynthesis,
- qP – photochemical quenching,
- qNP – non-photochemical quenching,
- ETR – electron flow rate through photosystems,
- Rfd – vitality index. A measure of potential photosynthetic activity under given light conditions and the interaction of the light-phase reaction with biochemical reactions in the dark phase of photosynthesis.

Statistical analyses

The experiments for determining strawberry fruit yield in the field experiment, the presence of arbuscular mycorrhizal fungi and chlorophyll fluorescence, were performed in four replications. The least significant differences (LSD) were calculated at the level of $p = 0.05$ for all experimental data. The results were statistically analysed by one-way analysis of variance in a random block design. Multiple comparisons of means for the combinations were performed with Tukey's test at a significance level of $\alpha = 0.05$ using STATISTICA v.13.3 software [TIBCO Software Inc., 2017].

RESULTS

Fruit yield of strawberry

The obtained results showed that irrigation with 100% supply of strawberry plants grown in the field significantly increased the fruit yield per plant in cultivars Rumba and Honeoye in comparison to irrigation with 50% water supply (Fig. 4). Additionally, the application of Inoculum 1 or 2 significantly increased the yield of the strawberry plant. The most beneficial effects were observed after the applications of Inoculum 1 and in Rumba plants grown under 100% water supply. Due to such treatments, the strawberry fruit

yield per plant increased by 8% compared to control plants. Under 50% water supply conditions, the most profitable result was noted after the treatment of Inoculum 2 with antagonistic properties against pathogens. Due to such treatment, the fruit yield increased by 4% compared to control. In the case of the cultivar Honeoye, the application of Inoculum 1 and 2 showed a tendency to increase the fruit yield of plants grown under irrigation with 100% water supply.

In the pot experiments, the yield of strawberry fruits of cultivars Rumba and Honeoye also depended on the irrigated regime (Fig. 5). Plants grown in fully irrigated (100% water supply) pots yielded much higher than plants irrigated with 50% water supply. Under the conditions of 100% water supply, the ap-

plication of Inoculum 2 was the most advantageous compared to control. It concerned both Rumba and Honeoye plants. However, plants grown in conditions with a 50% water supply yielded significantly higher after Inoculum 1 and 2 applications than those grown in the control.

The effects of bacterial inoculants on the presence of arbuscular mycorrhizal fungi growing in different irrigation regimes

The laboratory analyses of Rumba strawberry plants conducted in the field experiment showed that the roots treated with Inoculum 2 and grown under conditions of 50% of water supply were the most frequently and intensely colonised by arbuscular mycor-

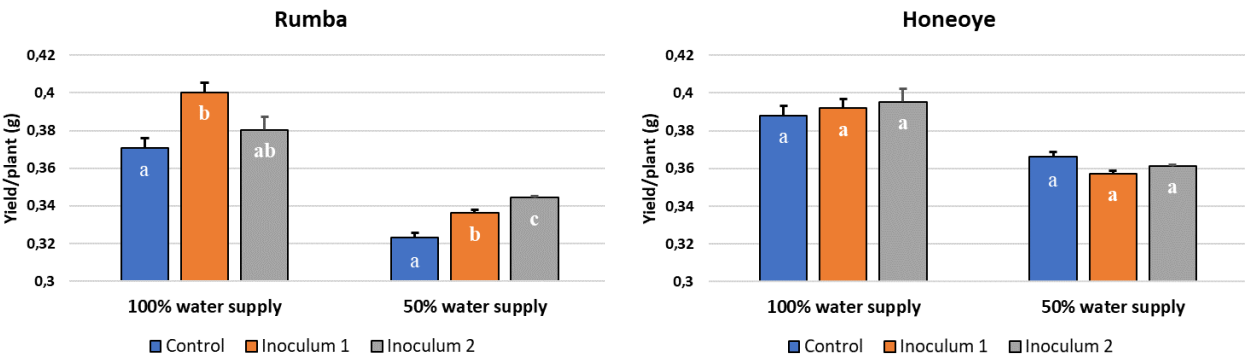


Fig. 4. In the field experiment (Ecological Experimental Field), the effect of microbiological inocula on the yield of Rumba and Honeoye cultivars of strawberry plants. The data within the variety and the irrigation regime, as well as with the same letter, do not differ significantly according to Tukey's test (5%). Values are the means of four replications, each comprising 75 plants

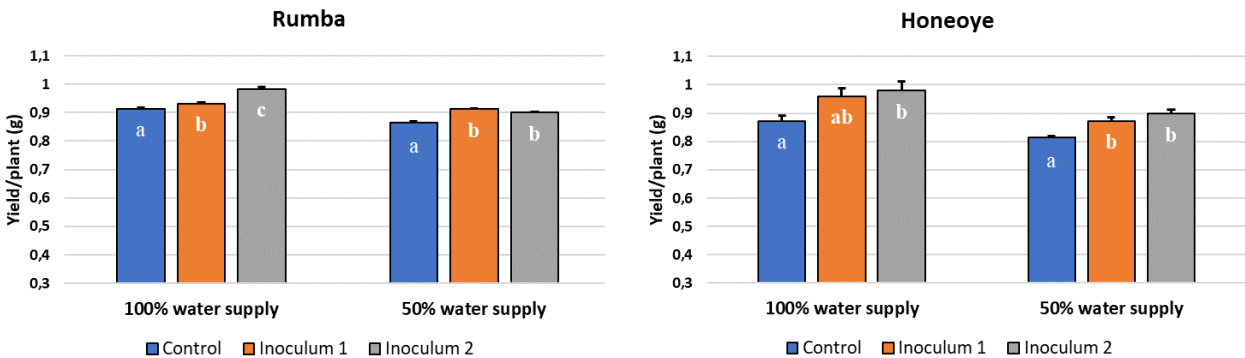


Fig. 5. In the pot experiment, the effect of microbiological inocula on the yield of Rumba and Honeoye cultivars of strawberry plants. The data within the variety and the irrigation regime, as well as with the same letter, do not differ significantly according to Tukey's test (5%). Values are the means of four replications, each comprising 75 plants

rhizal fungi (AMF – 62.22%) – Table 1, Figs 6–9. The application of Inoculum 1 also resulted in increased root colonisation by mycorrhizal fungi (52.22%). Similar beneficial results were also observed, but to a lesser extent, under 100% of water supply. After the application of Inoculum 2 and 1, the degree of mycorrhizal frequency (F%) increased to 51.11 and 42.22%, respectively.

As a result of the conducted laboratory analyses, it was observed – Figures 6–9.

Similar results were obtained in the case of Honeoye plants grown in the pot experiment (Table 2). The most pronounced effect was the application of Inoculum 2 with antagonistic properties against patho-

gens, both under 100% and 50% water supply. Due to such treatment, the colonisation of roots by arbuscular mycorrhizal fungi increased to 65.56 and 64.44%, respectively. The slight difference between the two conditions of water regimes (100% and 50% water supply) suggests that water supply did not affect the colonisation of roots by the arbuscular mycorrhizal fungi. Inoculum 2 had the most significant impact on mycorrhizal intensity in the roots of strawberry plants of the Honeoye variety. The application of Inoculum 1 also remarkably improved this parameter under 100% and 50% water supply. Due to such treatment, the colonisation of roots by arbuscular mycorrhizal fungi increased to 52.22 and 53.33%, respectively.

Table 1. The effect of treating strawberry plants of Rumba variety with microbial inocula, grown under various water conditions, on the degree of mycorrhizal frequency (F%), mycorrhizal intensity (m%, M%), and arbuscular abundance (a%, A%) in the field experiment. The data within the column and with the same letter, do not differ significantly according to Tukey’s test (5%)

Treatment	100% water					50% water				
	F%	M%	m%	a%	A%	F%	M%	m%	a%	A%
Control	27.78a	2.33a	8.39a	0	0	35.56ab	2.22ab	6.23a	0	0
Inoculum 1	42.22b	3.02a	7.17a	0	0	52.22c	3.34ab	6.34a	0	0
Inoculum 2	51.11c	3.71ab	7.29a	0	0	62.22d	4.74b	7.59a	0	0

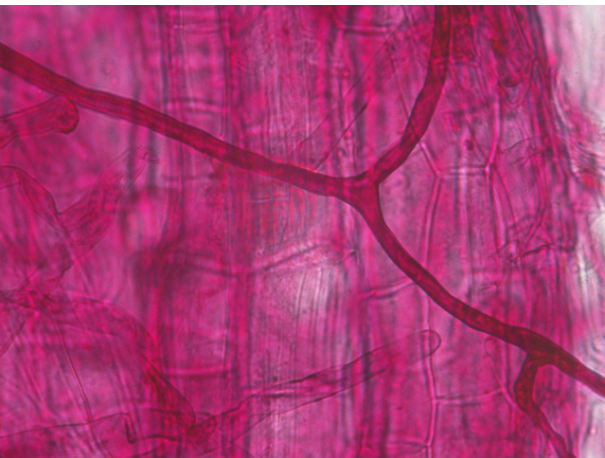


Fig. 6. Mycorrhizal hyphae in the roots of Rumba strawberry plants grown under 100% water supply conditions and treated with Inoculum 2 (field experiment)

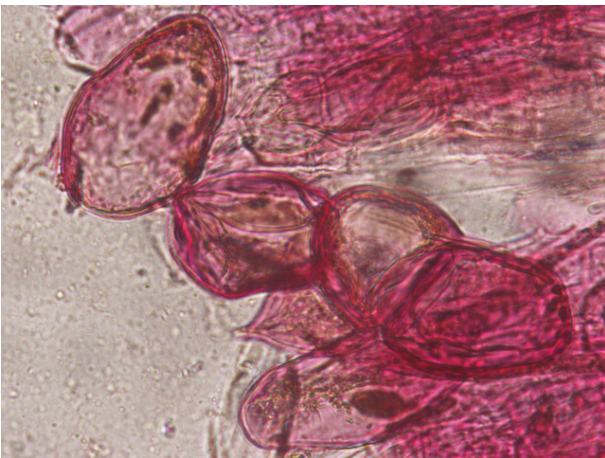


Fig. 7. Vesicle in the roots of Rumba strawberry plants grown under 100% water supply conditions and treated with Inoculum 2 (field experiment)

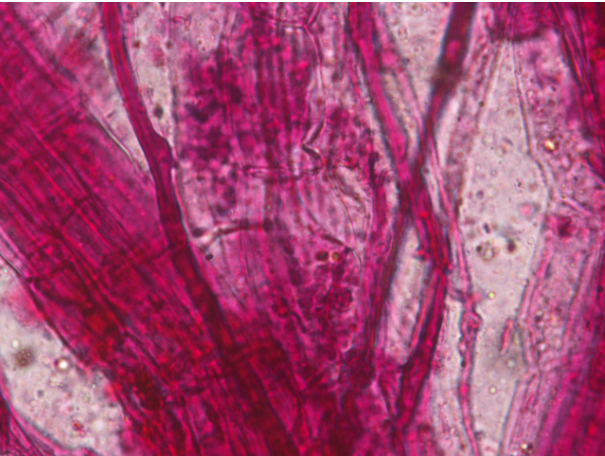


Fig. 8. Mycorrhizal hyphae in the roots of Rumba strawberry plants grown under 50% water supply and treated with Inoculum 2 (field experiment)

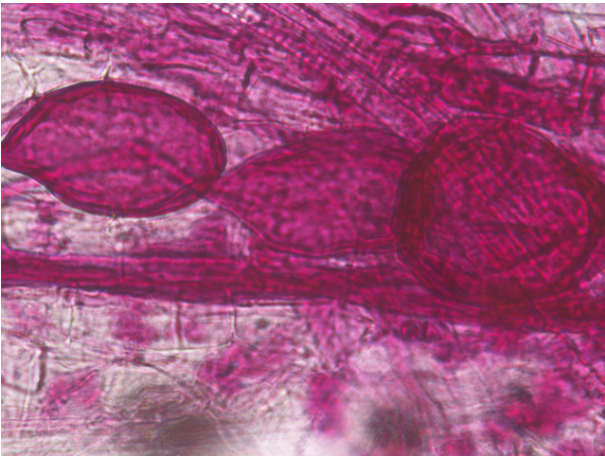


Fig. 9. Vesicles in the roots of Rumba strawberry plants grown under 50% water supply and treated with Inoculum 2 (field experiment)

Table 2. The influence of treating strawberry plants of the Honeoye variety with microbial inocula, grown under various water conditions, on the degree of mycorrhizal frequency (F%), mycorrhizal intensity (m%, M%), and arbuscular abundance (a%, A%) in the field experiment. The data within the column and with the same letter, do not differ significantly according to Tukey’s test (5%)

Treatment	100% water			50% water		
	F%	M%	m%	F%	M%	m%
Control	36.67a	3.43a	9.31a	34.45a	2.68a	7.81a
Inoculum 1	52.22b	4.50a	8.59a	53.33b	3.68a	6.90a
Inoculum 2	65.56c	4.67a	7.10a	64.44c	4.33a	6.67a

As a result of the conducted laboratory analyses, it was observed – Figures 10–13.

The laboratory results obtained from the pot experiment with Rumba demonstrated the highest abundance of arbuscula in the root cells due to the application of Inoculum 1 (Table 3). After treatment with these inocula, the abundance of arbuscula in the root cells increased both under 100% and 50% water supply to 40,96 and 29,09%, respectively. Additionally, the application of Inoculum 2 increased the degree of mycorrhizal association in plant roots both under 100% and 50% water supply. As a result of water restriction, the application of Inoculum 2 increased the

degree of mycorrhizal association in their roots. Under the influence of Inoculum 1 application, Rumba strawberry plant roots formed arbuscules with the highest abundance.

Similar results were obtained in the case of Honeoye plants grown in the pot experiment (Table 4, Figs 10–13). Inoculum 2 significantly increased the colonisation of roots by arbuscular mycorrhizal fungi. The applied plant watering method did not influence the obtained results. The enhancement of AMF colonisation and abundance of arbuscules in Rumba and Honeoye strawberries was observed particularly with Inoculum 2 under examined water regimes.

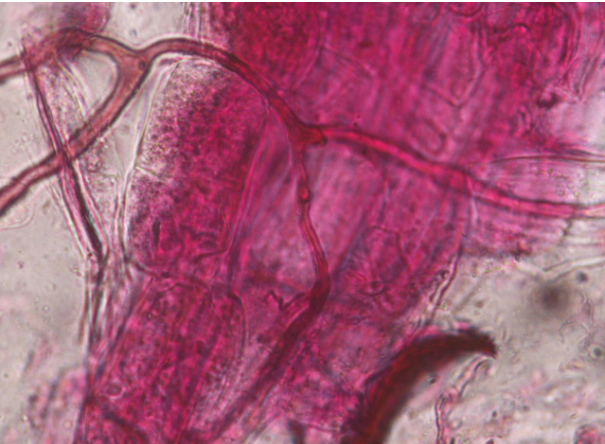


Fig. 10. Mycorrhizal hyphae in the roots of strawberry plants of Honeoye treated with Inoculum 2, grown under 100% water supply conditions (pot experiment)

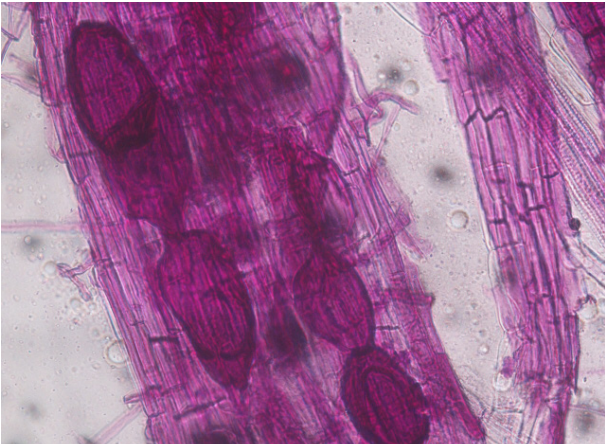


Fig. 11. Vesicles in the roots of strawberry plants of Honeoye treated with Inoculum 2, grown under 100% water supply conditions (pot experiment)

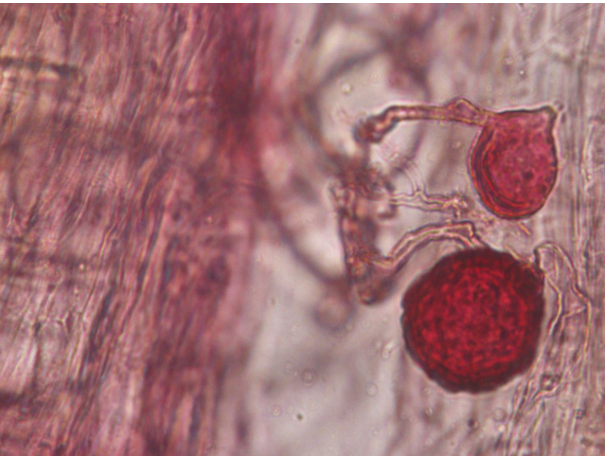


Fig. 12. Spores in the roots of strawberry plants of Honeoye variety treated with Inoculum 2, grown under 50% water supply conditions (pot experiment)

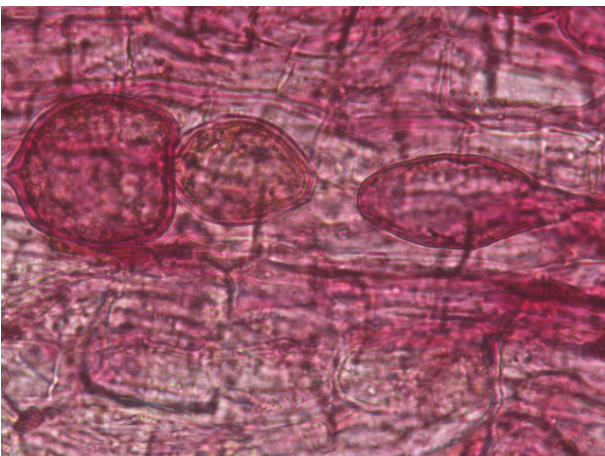


Fig. 13. Vesicles in the roots of strawberry plants of Honeoye variety treated with Inoculum 2, grown under 50% water supply conditions (pot experiment)

Table 3. Effect of treating Rumba variety strawberry plants with inocula of microorganisms growing in different water conditions on the presence of arbuscular mycorrhizal fungi in the roots in the pot experiment. The data within the column and with the same letter, do not differ significantly according to Tukey’s test (5%)

Treatment	100% water					50% water				
	F%	M%	m%	a%	A%	F%	M%	m%	a%	A%
Control	71.11a	6.24a	8.95a	34.05ab	2.23a	50.0a	4.48a	8.81a	14.19a	0.75a
Inoculum 1	68.69a	6.91a	10.01a	40.96b	2.90a	58.89a	4.98a	8.34a	29.09ab	1.45a
Inoculum 2	66.67a	6.25a	9.28a	39.0b	2.56a	66.67a	5.56a	8.43a	20.63ab	1.15a

Table 4. Effect of treating Honeoye variety strawberry plants with inocula of microorganisms growing in different water conditions on the presence of arbuscular mycorrhizal fungi in the roots in the pot experiment. The data within the column and with the same letter, do not differ significantly according to Tukey’s test (5%)

Treatment	100% water					50% water				
	F%	M%	m%	a%	A%	F%	M%	m%	a%	A%
Control	47.78a	3.77a	7.87a	9.70a	0.39a	47.78a	3.21a	6.63a	12.66a	0.39a
Inoculum 1	61.11bc	4.81ab	7.86a	30.62ab	1.48a	60.0ab	4.43ab	7.37a	16.78a	0.73a
Inoculum 2	78.89 c	7.65 b	9.69a	55.88 b	4.23 b	68.89bc	6.18ab	8.69a	37.94ab	2.48ab

The effects of bacterial inoculants application on the photosynthesis efficiency in strawberry leaves

In the field experiment with strawberry plants, the irrigation in 50% water supply negatively affected the maximum quantum yield of PSII (F_v/F_m) and quantum efficiency of photochemical reaction in PSII (Φ_{PSII}), photochemical quenching (qP) and the vitality index compared to plants irrigated in 100% supply (RDF) – Fig. 14. The most harmful effect of reduced irrigation was observed in Honeoye cultivar, which produced a significant decrease in F_v/F_m , Φ_{PSII} , qP and RDF.

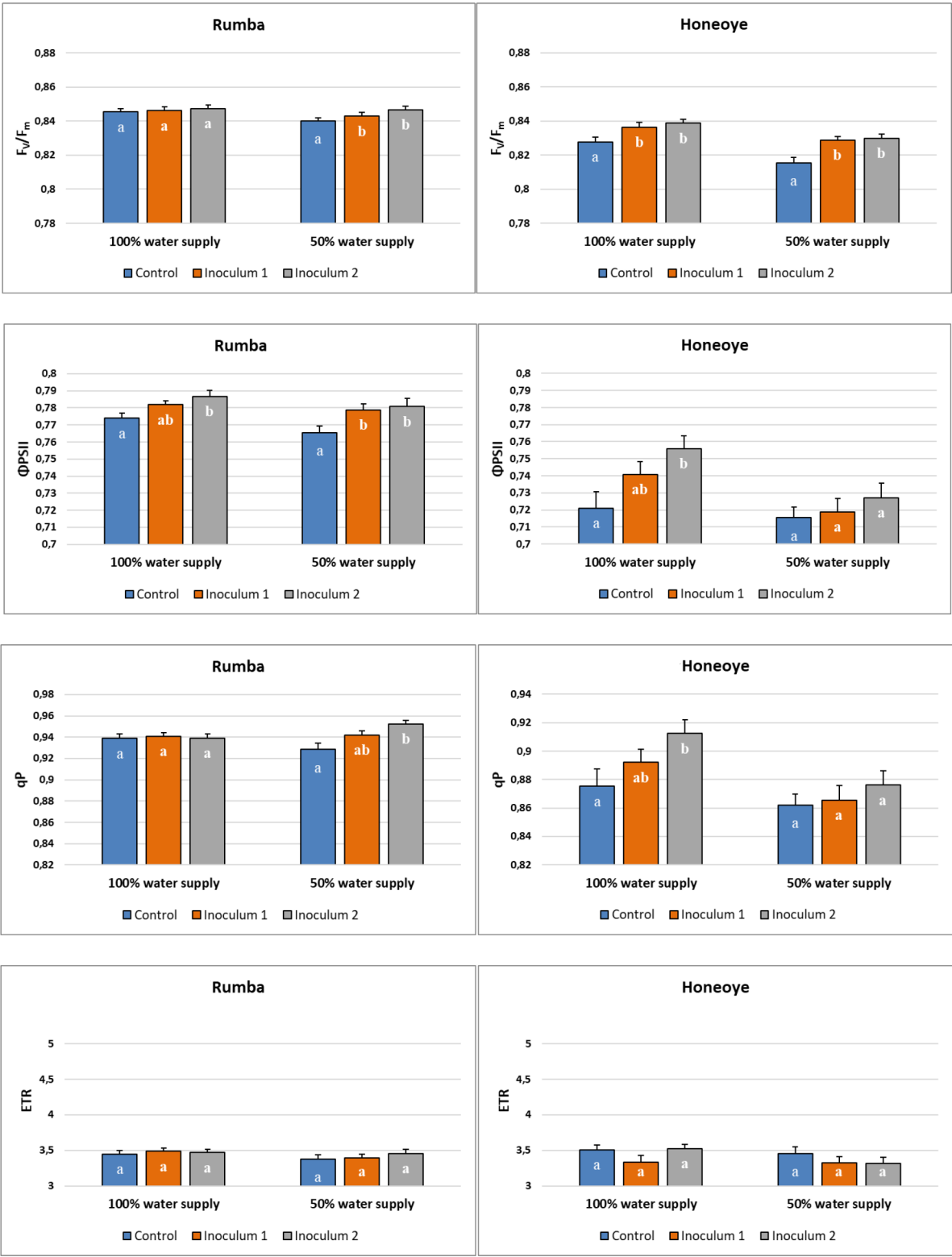
The application of Inoculum 1 and 2 positively affected Honeoye plants in both irrigated with 100% and 50% water supply plots. Its beneficial effects were visible in regard to the maximum efficiency of photochemical reaction (F_v/F_m), the quantum efficiency of photochemical reaction in PSII (Φ_{PSII}) and the maximum efficiency of water decomposition in PSII (F_v/F_0). In Rumba plants, the beneficial effect of both inocula applications was visible in irrigated in 50% water supply plots. Due to such treatments, the maximum quantum yield of PSII (F_v/F_m) and the maximum efficiency of water decomposition in PSII (F_v/F_0) were improved.

In the pot experiment, the irrigation regimes did not affect the parameters of fluorescence activity in leaves (RDF) – Fig. 15. However, the application of inocula positively affected the photosynthesis efficiency in both Rumba and Honeoye strawberry plants. Plant treatments with Inoculum 1, in most cases, stimulated the maximum efficiency of photochemical reaction (F_v/F_m), quantum efficiency of photochemical reaction in PSII (Φ_{PSII}), photochemical quenching (qP), electron flow rate through photosystems (ETR), maximum

efficiency of water decomposition in PSII (F_v/F_0) and the vitality index (Rfd). In the case of 50% water supply, the best effect was observed after Inoculum 2. Especially in Honeoye plants. Due to such treatment, maximum efficiency of photochemical reaction (F_v/F_m), quantum efficiency of photochemical reaction in PSII (Φ_{PSII}), photochemical quenching (qP), maximum efficiency of water decomposition in PSII (F_v/F_0) and the vitality index (Rfd).

DISCUSSION

The widespread occurrence of drought stress poses a significant threat to crop yields worldwide, leading to a substantial decrease in the productivity of many crops due to water scarcity [Song et al. 2023, Mazurek-Kusiak et al. 2021]. Moreover, drought stands out as one of the most significant environmental factors limiting the agricultural production of strawberries globally, adversely affecting the anatomical, physiological, and enzymatic characteristics of plants [Fig. 3; Khan 2023]. In strawberry plants, reduced irrigation typically leads to smaller fruit size and lower yield due to their shallow root system, large leaf area, and succulent texture. As a result, they are highly vulnerable to water deficiency-induced damage, which ultimately reduces biomass and crop yield [Zahedi et al. 2023]. Furthermore, plants are highly susceptible to mineral deficiencies caused by inadequate soil moisture and reduced mobilisation of minerals within plant tissues [Zahedi et al. 2023]. The results obtained from the present study clearly indicated that reducing the water supply to 50% significantly decreased the fruit yield per strawberry plant in cultivars Rumba and Honeoye



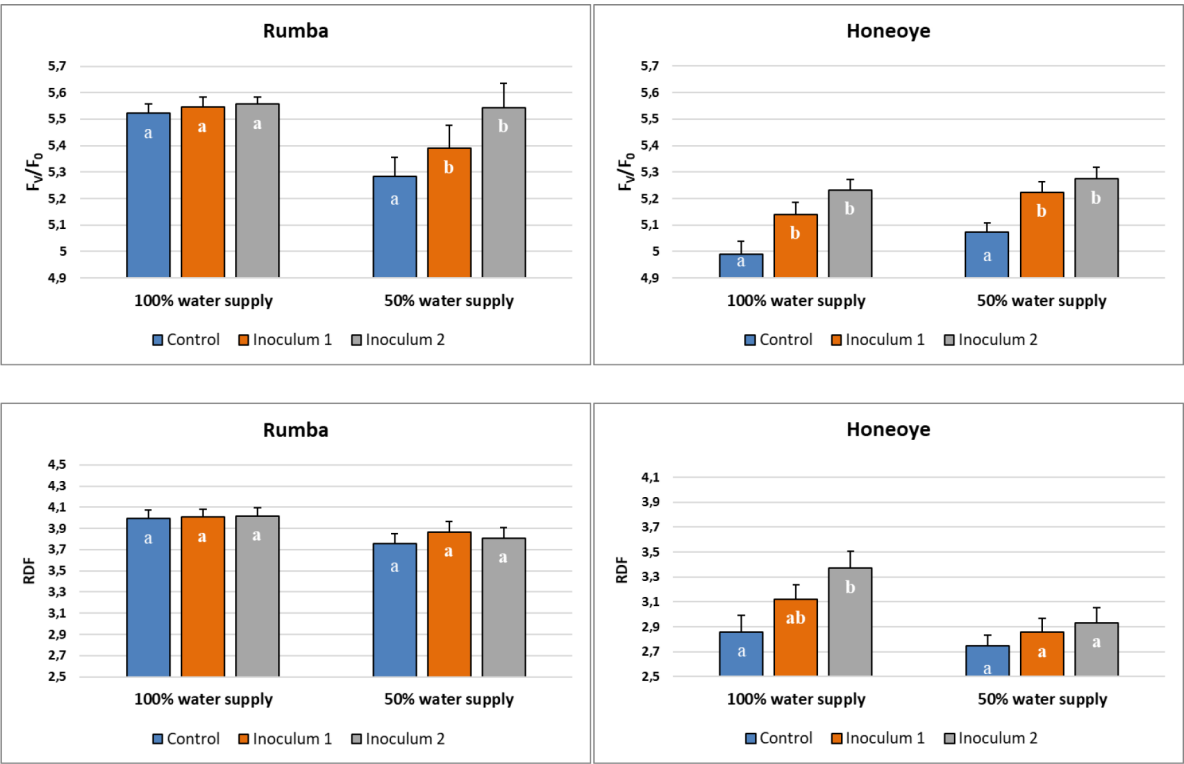
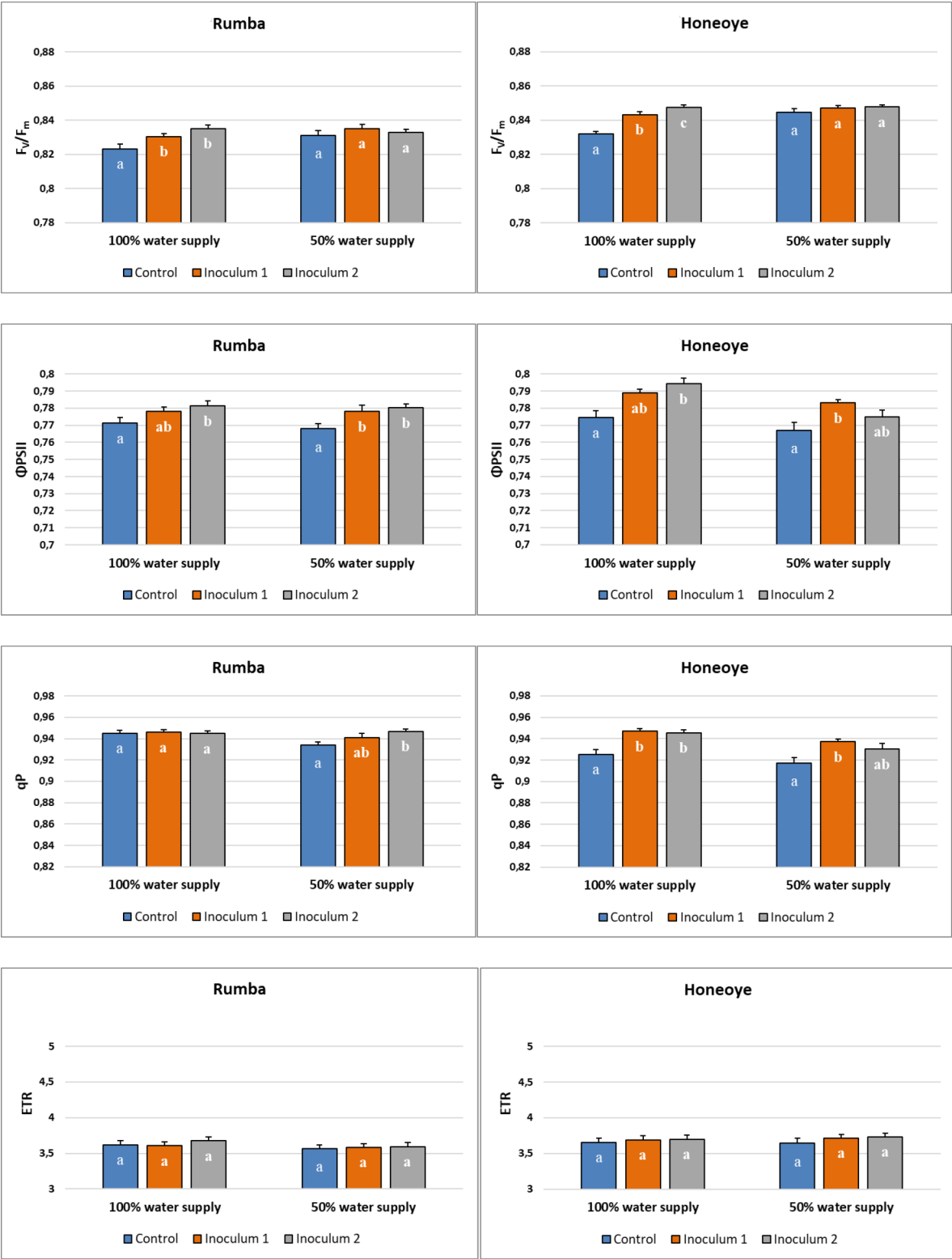


Fig. 14. The effect of microbiological inocula application in the field experiment on the photosynthesis efficiency of Rumba and Honeoye cultivars of strawberry plants in the field experiment. Maximum efficiency of photochemical reaction (F_v/F_m), quantum efficiency of photochemical reaction in PSII (Φ_{PSII}), photochemical quenching (qP), non-photochemical quenching (qNP), electron flow rate through photosystems (ETR), maximum efficiency of water decomposition in PSII (F_v/F_0) and the vitality index (Rfd). The data within the variety and with the same letter do not differ significantly according to Tukey's test (5%). Values are the means of four replications, each comprising 75 plants

compared to irrigation with 100% water supply. Furthermore, the diminishing water supply also caused a decrease in photosynthesis efficiency expressed by fluorescence activity in leaves. This was observed both in the field and pot conditions.

However, the present study showed that the application of Inoculum 1 (C09EX – *Pseudomonas* sp., Ps150AB *Pseudomonas* sp.) or 2 (JAFGU – *Lyso*bacter sp.) significantly increased the fruit yield of strawberry plants. The most beneficial effects were observed after applying Inoculum 1 to Rumba plants grown under 100% water supply. Under 50% water supply conditions, the most profitable outcome was observed following treatment by Inoculum 2. Apply-

ing Inoculum 1 and 2 increased fruit yield in Honeoye cultivar plants grown with 100% water supply. Previous research also showed that the treatments of strawberry roots with SP116AC and JaFGU (*Lyso*bacter sp.) resulted in a significant increase in the total leaf surface, the total length of roots, and their total surface area [Trzciński et al. 2021]. In pot experiments, the application of Inoculum 2 was beneficial under full irrigation, while the applications of Inoculum 1 and 2 increased yields similarly under 50% irrigation. Wang et al. [2024] also reported that *Pseudomonas fluorescens* could enhance biofilm formation and rhizosphere colonisation, which was probably essential in promoting strawberry growth.



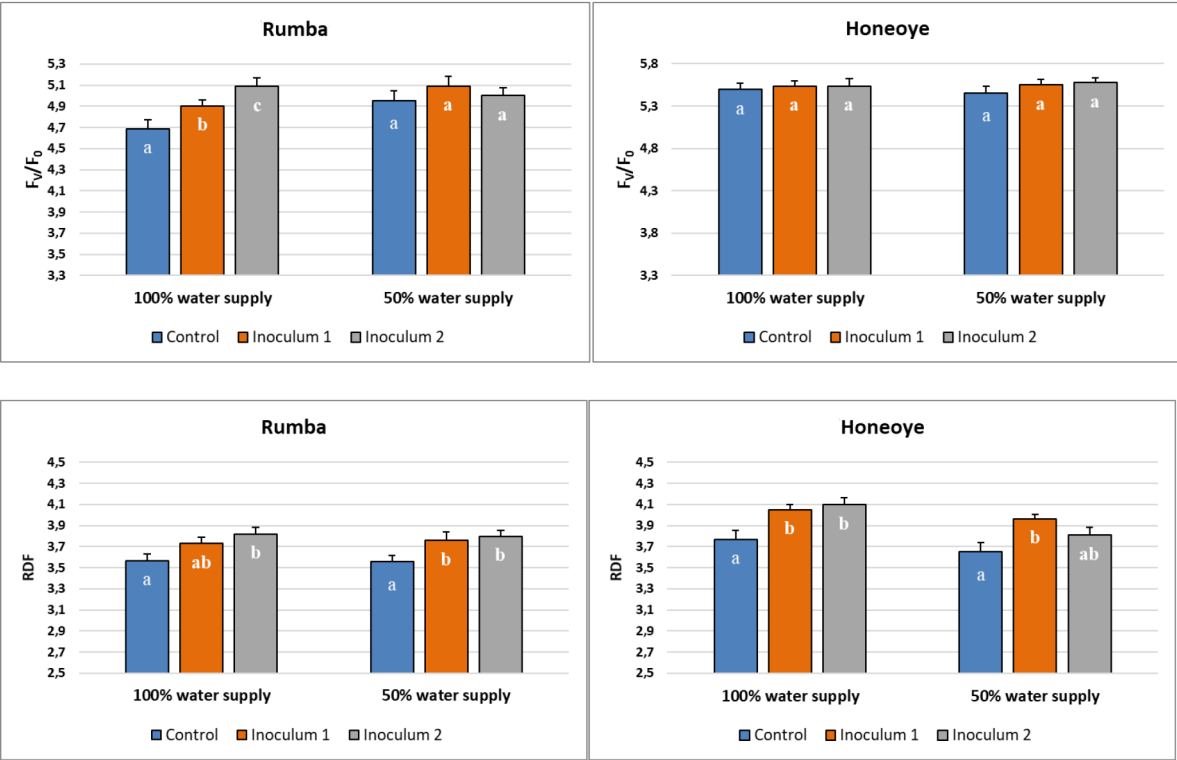


Fig. 15. The effect of microbiological inocula on photosynthesis efficiency on the basis of fluorescence activity in leaves of Honeoye cultivars in the pot experiment. Maximum efficiency of photochemical reaction (F_v/F_m), quantum efficiency of photochemical reaction in PSII (Φ_{PSII}), photochemical quenching (qP), non-photochemical quenching (qNP), electron flow rate through photosystems (ETR), maximum efficiency of water decomposition in PSII (F_v/F_0) and the vitality index (Rfd). The data within the variety and with the same letter do not differ significantly according to Tukey's test (5%). Values are the means of 7 replications, each comprising 3 plants

The study demonstrated the significant impact of microbial inocula on the root colonisation of Rumba and Honeoye strawberry plants. Inoculum 2, especially under reduced water supply, resulted in the highest levels of AMF colonisation in Rumba plants. This indicates that water stress might enhance mycorrhizal effectiveness. Inoculum 1 also increased AMF colonisation, though less effectively than Inoculum 2. Interestingly, no arbuscules were observed in the root segments of Rumba plants, suggesting that specific conditions may have resulted in their complete absence. Similar beneficial effects of the inoculants were noted in Honeoye plants, with Inoculum 2 showing the most pronounced impact on AMF colonisation re-

gardless of water supply levels. The slight differences between the water regimes indicate that water availability had minimal effect on AMF colonisation in Honeoye plants. The pot experiment further supported these findings, with Inoculum 1 significantly increasing the abundance of arbuscules in Rumba roots. Both inocula improved mycorrhizal associations in Honeoye roots, with Inoculum 2 having a notable impact on mycorrhizal intensity and arbuscule abundance. These findings suggest that water stress may enhance AMF colonisation, particularly with Inoculum 2, offering strategies to improve strawberry resilience and adaptability under varying water availability. Chiomento et al. [2019, 2021] also reported that inoculation with

arbuscular mycorrhizal fungi improves strawberry growth and development, yield, fruit quality and overall performance, leading to more profuse root systems and increased fruit anthocyanin content. Similar to the findings on Rumba plants, it has been shown that water stress can enhance AMF colonisation. For instance, a study by Borowicz [2010] observed that AMF can improve water relations, thereby increasing the host plant's tolerance to drought stress. Hernández-Sebastià et al. [1999] demonstrated that AMF colonisation could improve water content in strawberry plants, leading to better water status and higher relative water content (RWC) under high humidity conditions. Hernández-Sebastià et al. [2000] found also that strawberry plantlets inoculated with AMF had distinct amino acid and starch concentration changes under water stress compared to non-mycorrhizal plants, suggesting specialised adaptation strategies. Research by Zhu et al. [2010] on maize showed that AMF symbiosis improves plant growth, water status, and photosynthetic capacity under stress conditions. The absence of arbuscules in Rumba plants under specific conditions suggests that environmental factors and the type of AMF can influence arbuscule formation. Moradtalab et al. [2019] demonstrated that both AMF and silicon could synergistically enhance strawberry plant growth under drought by increasing mycorrhizal intensity and nutrient uptake, indicating complex interactions affecting arbuscule formation. The observed enhancement of AMF colonisation in Rumba and Honeoye strawberries under different water regimes, particularly with Inoculum 2, is consistent with the broader scientific literature. Water stress appears to enhance AMF effectiveness, offering potential strategies for improving plant resilience and adaptability [Pérez-Moncada et al. 2024, Raturi et al. 2023, Silva et al. 2023].

The presented data indicated that reduced irrigation significantly impaired several parameters associated with photosynthetic efficiency in strawberry plants, especially in Honeoye cultivar. This negative impact is evident in the decreased maximum quantum yield of PSII (F_v/F_m) and quantum efficiency of photochemical reaction in PSII (Φ_{PSII}), as well as diminished photochemical quenching (qP) and vitality index (Rfd). In a study by El-Beltagi et al. [2022], drought stress (40% and 80%) led to decreased net photosynthetic

rate, stomatal conductance and transpiration rate. The present findings suggest that Honeoye is particularly susceptible to water stress, which emphasises the importance of adequate irrigation for maintaining its photosynthetic performance. Conversely, the application of Inoculum 1 and Inoculum 2 showed positive effects on the photosynthetic efficiency of both Honeoye and Rumba cultivars under varying irrigation conditions. These inocula appear to mitigate the adverse effects of water deficit, as demonstrated by the improved F_v/F_m , Φ_{PSII} , and F_v/F_0 values in treated plants. In particular, the positive impact of inocula was more evident in Honeoye plants exposed to 50% reduction in water supply, emphasising their potential to improve drought resistance. Valle-Romero et al. [2023] have found that biofertilisation with plant growth-promoting bacteria (PGPB) improves the photosynthetic efficiency of strawberry plants under water stress by increasing the net photosynthetic rate and intrinsic water use efficiency.

In the pot experiments, where irrigation regimes did not influence fluorescence parameters, the positive role of the inocula in enhancing photosynthetic efficiency was still evident. It suggests that the application of these inocula can stimulate photosynthetic efficiency regardless of irrigation conditions. Inoculum 1 consistently stimulated parameters such as F_v/F_m , Φ_{PSII} , qP, electron flow rate (ETR), F_v/F_0 , and the vitality index (Rfd) in leaves of both cultivars. The importance of arbuscular mycorrhizal fungi (AMF) in enhancing the photosynthetic efficiency of micropropagated strawberry plants under drought stress in greenhouse conditions has been emphasised [Borkowska 2002]. It was suggested that the main limitation under relatively severe conditions was stomatal closure due to photosynthetic limitations [Yokoyama et al. 2023].

Under reduced water supply conditions, Inoculum 2 appeared as especially effective in improving the photosynthetic parameters in Honeoye plants. It indicated that specific microbial inocula can offer benefits depending on the cultivar and environmental stressors. The improvement in quantum efficiency, photochemical quenching, and vitality index in Inoculum 2-treated plants suggests a potential strategy for maintaining high photosynthetic efficiency under suboptimal irrigation. This novelty of the present research includes

the identification of specific microbial inocula that improved strawberry fruit yield, AMF colonisation and photosynthetic efficiency, especially under water stress conditions, providing innovative strategies for improving crop resilience and productivity.

Further research is needed to explore the underlying mechanisms by which these inocula enhance the yield of strawberry fruit, the efficiency of photosynthesis in leaves, and arbuscular mycorrhizal fungi, especially for vulnerable varieties to water stress. The research also shows the potential of using microbial inocula to mitigate the adverse effects of reduced irrigation. Further research is needed to understand how these interventions enhance plant productivity under varying environmental conditions. These findings contribute to the knowledge of sustainable agriculture and the use of inocula to improve crop resilience to environmental stressors.

CONCLUSIONS

The presented study provides substantial evidence of the critical role that irrigation regimes and microbial inocula play in influencing the productivity, root mycorrhizal colonisation, and photosynthetic efficiency of strawberry plants. The results indicate that full irrigation (100% water supply) significantly increased fruit yield compared to reduced irrigation (50% water supply). Applying bacterial inoculants, specifically Inoculum 1 (*Pseudomonas* spp.) and Inoculum 2 (*Lysobacter* sp.), further enhances yield, with Inoculum 1 being most effective under full irrigation and Inoculum 2 under reduced irrigation. Root colonisation by arbuscular mycorrhizal fungi (AMF) was markedly improved by both inocula, particularly Inoculum 2, irrespective of the irrigation level, suggesting its potential role in enhancing plant resilience to water stress. Photosynthetic efficiency parameters, including the maximum quantum yield of PSII (F_v/F_m) and quantum efficiency of photochemical reaction in PSII (Φ_{PSII}), were significantly impaired by reduced irrigation, especially in the Honeoye cultivar. However, these adverse effects were substantially mitigated by applying microbial inocula, which improved photosynthetic performance under both irrigation regimes. These findings emphasise the potential of microbial inocula as a sustainable agricultural strategy to miti-

gate the adverse effects of water scarcity on strawberry plants. Future research should focus on elucidating the underlying mechanisms by which these inocula enhance plant productivity and resilience under various environmental conditions, thereby optimising their application for diverse agricultural practices.

SOURCE OF FUNDING

The research was supported by the National Centre for Research and Development under BIO-STRATEG program, contract number BIOSTRATEG/344433/16/NCBR/2018 conducted at the National Institute of Horticultural Research in Skierniewice.

REFERENCES

- Azam M., Ejaz S., Naveed Ur Rehman R., Khan M., Qadri R. (2019). Postharvest Quality Management of Strawberries. In: Asao T, Asaduzzaman M (eds), Strawberry. Pre-and post-harvest management techniques for higher fruit quality. IntechOpen. <https://dx.doi.org/10.5772/intechopen.82341>
- Borkowska B. (2002). Growth and photosynthetic activity of micropropagated strawberry plants inoculated with endomycorrhizal fungi (AMF) and growing under drought stress. *Acta Physiol. Plant.* 24, 365–370. <https://doi.org/10.1007/s11738-002-0031-7>
- Borowicz V.A. (2010). The impact of arbuscular mycorrhizal fungi on strawberry tolerance to root damage and drought stress. *Pedobiologia* 53(4), 265–270. <https://doi.org/10.1016/j.pedobi.2010.01.001>
- Cecatto A.P., Ruiz F.M., Calvete E.O., Martínez J., Palencia P. (2016). Mycorrhizal inoculation affects the phytochemical content in strawberry fruits. *Acta Sci. Agron.* 38, 227–237. <https://doi.org/10.4025/actasciagron.v38i2.27932>
- Chen S., Zhao H., Zou C., Li Y., Chen Y., Wang Z., Jiang Y., Liu A., Zhao P., Wang M., Ahammed G.J. (2017). Combined Inoculation with Multiple Arbuscular Mycorrhizal Fungi Improves Growth, Nutrient Uptake and Photosynthesis in Cucumber Seedlings. *Front. Microbiol.* 8, 2516. <https://doi.org/10.3389/fmicb.2017.02516>
- Chiomento J.L.T., da Costa R.C., de Nardi F.S., Trentin N. dos S., Nienow A.A., Calvete E.O. (2019). Arbuscular mycorrhizal fungi communities improve the phytochemical quality of strawberry. *J. Hortic. Sci. Biotechnol.* 94(5), 653–663. <https://doi.org/10.1080/14620316.2019.1599699>

- Chiomento J.L.T., Fracaro J., Görgen M., Fante R., Dal Pizzol E., Welter M., Klein A.P., Trentin T.S., Suzana-Milan C.S., Palencia P. (2024) Arbuscular Mycorrhizal Fungi, *Ascophyllum nodosum*, *Trichoderma harzianum*, and their combinations influence the phyllochron, phenology, and fruit quality of strawberry plants. *Agronomy* 14:860. doi:10.3390/agronomy14040860
- Chiomento J.L.T., de Paula J.E.C., de Nardi F.S., Trentin T. dos S., Magro F.B., Dornelles A.G., Anzolin J., Fornari M., Trentin N. dos S., Rizzo L.H., Calvete E.O. (2021). Arbuscular mycorrhizal fungi influence the horticultural performance of strawberry cultivars. *Res. Soc. Dev.* 10(7), e45410716972. <https://doi.org/10.33448/rsd-v10i7.16972>
- Derkowska E., Sas-Paszt L., Dyki B., Sumorok B. (2015). Assessment of mycorrhizal frequency in the roots of fruit plants using different dyes. *Advances in Microbiology*. 5, 54–64. <http://creativecommons.org/licenses/by/4.0/>
- El-Beltagi H.S., Ismail S.A., Ibrahim N.M., Shehata W.F., Alkhateeb A.A., Ghazzawy H.S., El-Mogy M.M., Sayed E.G. (2022). Unravelling the effect of triacontanol in combating drought stress by improving growth, productivity, and physiological performance in strawberry plants. *Plants* 11, 1913. <https://doi.org/10.3390/plants11151913>
- FAO 2023. Food and Agriculture Organization of the United Nations. Crops and livestock products. <https://www.fao.org/faostat/en/#data/QCL>.
- Haghshenas M., van Delden S.H., Nazarideljou M.J. (2024). Effects of nutrient solution strength, PGPB, and mycorrhizal inoculation on growth, yield, and quality of strawberry. *Turk. J. Agr. For.* 48(3), 390–401. <https://doi.org/10.55730/1300-011X.3189>
- Hernández-Sebastià C., Samson G., Bernier P-Y., Piché Y., Desjardins Y. (2000). *Glomus intraradices* causes differential changes in amino acid and starch concentrations of *in vitro* strawberry subjected to water stress. *New Phytol.* 148(1), 177–186. <https://doi.org/10.1046/j.1469-8137.2000.00744.x>
- Hernández-Sebastià C., Piché Y., Desjardins Y. (1999). Water relations of whole strawberry plantlets *in vitro* inoculated with *Glomus intraradices* in a tripartite culture system. *Plant Sci.* 143(1), 81–91. [https://doi.org/10.1016/S0168-9452\(99\)00014-X](https://doi.org/10.1016/S0168-9452(99)00014-X)
- Jamiołkowska A., Skwaryło-Bednarz B., Patkowska E., Buczkowska H., Gałązka A., Grządziel J., Kopacki M. (2020). Effect of Mycorrhizal Inoculation and Irrigation on Biological Properties of Sweet Pepper Rhizosphere in Organic Field Cultivation. *Agronomy* 10(11), 1693. <https://doi.org/10.3390/agronomy10111693>
- Khan M.N. (2023). Melatonin regulates mitochondrial enzymes and ascorbate–glutathione system during plant responses to drought stress through involving endogenous calcium. *S. Afr. J. Bot.* 162, 622–632. <https://doi.org/10.1016/j.sajb.2023.09.032>
- Lane D.J. (1991). 16S/23S rRNA sequencing, pp. 115–175. In: Stackebrandt E. and M. Goodfellow (eds). *Nucleic acid techniques in bacterial systematics*. John Wiley & Sons Ltd, Chichester, United Kingdom.
- Mazurek-Kusiak A., Sawicki B., Kobyłka A. (2021). Contemporary challenges to the organic farming: a Polish and Hungarian case study. *Sustainability* 13(14), 8005. <https://doi.org/10.3390/su13148005>
- Mei C., Amaradasa B.S., Chretien R.L., Liu D., Snead G., Samtani J.B., Lowman S. (2021). A potential application of endophytic bacteria in strawberry production. *Horticulturae* 7(11), 504. <https://doi.org/10.3390/horticulturae7110504>
- Moradtalab N., Hajiboland R., Aliasgharzad N., Hartmann T.E., Neumann. G. (2019). Silicon and the association with an arbuscular-mycorrhizal fungus (*Rhizophagus clarus*) mitigate the adverse effects of drought stress on strawberry. *Agronomy* 9(1), 41. <https://doi.org/10.3390/agronomy9010041>
- Morais M.C., Mucha Â., Ferreira H., Gonçalves B., Bacelar E., Marques G. (2019). Comparative study of plant growth-promoting bacteria on the physiology, growth and fruit quality of strawberry. *J. Sci. Food Agric.* 99(12), 5341–5349. <https://doi.org/10.1002/jsfa.9773>
- Oregel-Zamudio E., Angoa-Pérez M.V., Oyoque-Salcedo G., Aguilar-González C.N., Mena-Violante H.G. (2017). Effect of candelilla wax edible coatings combined with biocontrol bacteria on strawberry quality during the shelf-life. *Sci. Hort.* 214, 273–279. <https://doi.org/10.1016/j.scienta.2016.11.038>
- Paliwoda D., Mikiciuk G., Mikiciuk M., Kisiel A., Sas-Paszt L., Miller T. (2022). Effects of rhizosphere bacteria on strawberry plants (*Fragaria × ananassa* Duch.) under water deficit. *Int. J. Mol. Sci.* 23(18), 10449. <https://doi.org/10.3390/ijms231810449>
- Pérez-Moncada U.A., Santander C., Ruiz A., Vidal C., Santos C., Cornejo P. (2024). Design of microbial consortia based on arbuscular mycorrhizal fungi, yeasts, and bacteria to improve the biochemical, nutritional, and physiological status of strawberry plants growing under water deficits. *Plants* 13(11), 1556. <https://doi.org/10.3390/plants13111556>
- Raturi P., Rai R., Sharma A.K., Singh A.K., Dimri D.C., Bains G. (2023). Effects of plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi

- (AMF) on morpho-physiological parameters of strawberry cv. Chandler under different moisture levels. *Int. J. Environ. Clim. Change*. 13(9), 2707–2713. <https://doi.org/10.9734/ijecc/2023/v13i92502>
- Redondo-Gómez S., García-López J.V., Mesa-Marín J., Pajuelo E., Rodríguez-Llorente I.D., Mateos-Naranjo E. (2022). Synergistic effect of plant-growth-promoting rhizobacteria improves strawberry growth and flowering with soil salinization and increased atmospheric CO₂ levels and temperature conditions. *Agronomy* 12(9), 2082. <https://doi.org/10.3390/agronomy12092082>
- Sahana B.J., Madaiah D., Sridhara S., Pradeep S., Nithin K.M. (2020). Study on effect of organic manures on quality and biochemical traits of strawberry (*Fragaria × ananassa* Duch.) under naturally ventilated polyhouse. *Int. J. Curr. Microbiol. Appl. Sci.* 9 (10), 2692–2698. <https://doi.org/10.20546/ijcmas.2020.910.325>
- Shahrajabian M.H., Petropoulos S.A., Sun W. (2023). Survey of the Influences of Microbial Biostimulants on Horticultural Crops: Case Studies and Successful Paradigms. *Hortic.* 9(2), 193. <https://doi.org/10.3390/horticulturae9020193>
- Sharma K., Mirza A.A., Aarti. (2023). Micronutrient and Metabolic Profiling of Strawberry Cultivars Grown in Subtropical Conditions: A Review. *Agric. Rev.* 46(3), 437–443. <https://doi.org/10.18805/ag.R-2642>
- Silva A.M.M., Feiler H.P., Qi X., Araújo V.L.V.P. de, Lacerda-Júnior G.V., Fernandes-Júnior P.I., Cardoso E.J.B.N. (2023). Impact of water shortage on soil and plant attributes in the presence of arbuscular mycorrhizal fungi from a harsh environment. *Microorganisms* 11(5), 1144. <https://doi.org/10.3390/microorganisms11051144>
- Song W., Song R., Zhao Y., Zhao Y. (2023). Research on the characteristics of drought stress state based on plant stem water content. *Sustain. Energy Technol. Assess.* 56, 103080. <https://doi.org/10.1016/j.seta.2023.103080>
- TIBCO Software Inc. (2017). Statistica (data analysis software system), version 13. <http://statistica.io>.
- Todeschini V., AitLahmidi N., Mazzucco E., Marsano F., Gosetti F., Robotti E., Bona E., Massa N., Bonneau L., Marengo E., Wipf D., Berta G., Lingua G. (2018). Impact of Beneficial Microorganisms on Strawberry Growth, Fruit Production, Nutritional Quality, and Volatilome. *Front. Plant Sci.* 9, 1611. <https://doi.org/10.3389/fpls.2018.01611>
- Trouvelot A., Kough J.L., Gianinazzi-Pearson V. (1986). Mesure du taux de mycorhization VA d'un système radiculaire. Recherche de méthodes d'estimation ayant une signification fonctionnelle. In: Gianinazzi-Pearson V. and Gianinazzi, S., Eds, *Physiological and Genetical Aspects of Mycorrhizae*, INRA, Paris, 217–221.
- Trzcíński P., Frąc M., Lisek A., Przybył M., Frąc M., Sas-Paszt L. (2021). Growth promotion of raspberry and strawberry plants by bacterial inoculants. *Acta Sci. Pol. Hortorum Cultus*. 20(6), 71–82. <https://doi.org/10.24326/asphc.2021.6.8>
- Valle-Romero P., García-López J.V., Redondo-Gómez S., Flores-Duarte N.J., Rodríguez-Llorente I.D., Idaszkin Y.L., Pajuelo E., Mateos-Naranjo E. (2023). Biofertilization with PGP bacteria improve strawberry plant performance under sub-optimum phosphorus fertilization. *Agronomy* 13(2), 335. <https://doi.org/10.3390/agronomy13020335>
- Wang Q., Chu C., Zhao Z., Wu S., Zhou D. (2024). *Pseudomonas fluorescens* enriched by *Bacillus velezensis* containing agricultural waste promotes strawberry growth by microbial interaction in plant rhizosphere. *Land Degrad. Dev.* 35(7), 2476–2488. <https://doi.org/10.1002/ldr.5074>
- Yokoyama G., Ono S., Yasutake D., Hidaka K., Hirota T. (2023). Diurnal changes in the stomatal, mesophyll, and biochemical limitations of photosynthesis in well-watered greenhouse-grown strawberries. *Photosynthetica* 61(1), 1–12. <https://doi.org/10.32615/ps.2023.001>
- Zahedi S.M., Hosseini M.S., Fahadi Hoveizeh N., Kadkhodaei S., Vaculik M. (2023). Physiological and biochemical responses of commercial strawberry cultivars under optimal and drought stress conditions. *Plants* 12(3), 496. <https://doi.org/10.3390/plants12030496>
- Zhu X.C., Song F.B., Xu H.W. (2010). Arbuscular mycorrhizae improves low temperature stress in maize via alterations in host water status and photosynthesis. *Plant Soil*. 331, 129–137. <https://doi.org/10.1007/s11104-009-0239-z>

