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ORIGINAL PAPER

Melanoidins promote growth in di- and monocotyledon plant species and drought tolerance in tomato plants

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Running title: Melanoidins effect on plant growth

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Abstract

Melanoidins (M), macromolecular nitrogenous products of the non-enzymatic Maillard reaction, were recently shown to be broad-spectrum inducers of plant immunity, effective against a diverse array of pathogens and plant hosts. While M-mediated protection is primarily facilitated through the salicylic acid (SA) pathway and defense priming, a persistent challenge in agriculture is the growth-defense trade-off, where the metabolic costs of immunity typically limit plant development. The aim of the present research was to investigate the bio-stimulant properties of M, a chemically characterized L-glutamic acid–D-glucose melanoidin preparation, and its capacity to promote growth in the absence of pathogen pressure. We demonstrate that M consistently enhances vegetative and reproductive growth across diverse crops, including indeterminate tomato, cucumber, sweet basil, lettuce, and wheat. Weekly applications of M via canopy spray or root drench significantly increased plant height, node formation, and leaflet area. In tomato and wheat, M treatment improved reproductive parameters, including fruit set, total fruit weight, and the number of spikes and tillers. Additionally, we report a significant novel role for M in alleviating abiotic stress; M-treated tomato plants continued to grow, wilted less and recovered better after rewatering under severe drought. These results position M as a versatile bio-stimulant and priming agent. Due to its high water solubility, ease of synthesis, and dual efficacy in biotic and abiotic stress management, M represents a robust candidate for sustainable agriculture and integrated disease management programs.

Keywords Melanoidins, Maillard reaction, SAR, eudicots, monocots, biostimulant, drought

Introduction

Global agriculture faces the dual challenge of escalating pathogen pressure and increasingly frequent abiotic stresses, such as drought, driven by climate change. Traditional reliance on chemical pesticides and synthetic fertilizers has raised significant environmental and health concerns, prompting an interest in natural inducers of plant resistance. Historically, chemical agents such as acibenzolar-S-methyl (ASM; Bion) and strobilurins have been deployed to activate plant defenses; however, while highly effective at inducing resistance, these chemicals, particularly ASM, are often associated with growth and yield penalties (Yassin et al. 2021; Leibman-Markus et al. 2023). Conversely, certain strobilurins like pyraclostrobin have been reported to improve plant health and yield even in the absence of disease pressure (Yassin et al. 2021). In tandem with chemical inducers, biological agents like *Bacillus* spp., *Pseudomonas* spp., and *Trichoderma* spp. have been described in some works as "twin service providers" capable of simultaneously enhancing both plant growth and immunity (Gupta and Bar 2020; Gupta et al. 2022c; Gupta et al. 2024; Leibman-Markus et al. 2023; Srivastava et al. 2026), thus avoiding the yield penalties often associated with the induction of plant immunity, and suggesting a potential use for such biological agents in agriculture. These biologicals often function through nutrient solubilization and the production of phytohormones like auxins and cytokinins, which improve root architecture and shoot development (Gupta et al. 2020; Gupta et al. 2023). Natural biopolymers like chitosan further exemplify this dual role, acting as non-toxic elicitors that promote growth by influencing cell division and nutrient uptake while suppressing a broad range of pathogens (Chakraborty et al. 2020).

Plant growth promotion has been commonly associated with introduced bacteria and fungi. For instance, root and shoot weight of tomato and tobacco were increased by introduction of *Trichoderma harzianum* and *T. koningii* into autoclaved soil (Windham et al. 1986). Promotion of tomato growth was observed in response to *Burkholderia tropica* that ultimately caused yield

increase in this crop (Bernabeu et al. 2015). Pseudomonad strains were reported to promote growth and yield of winter wheat (Freitas and Germida, 1992). Additionally, the ability of wheat plants to withstand water stress was enhanced by applying the bacteria *Bacillus safensis* and *Ochrobactrum pseudogregnonense*, which also function as plant growth promoting rhizobacteria (PGPR) (Chakraborty et al. 2013). Induced systemic resistance (ISR) by isolates of *Bacillus* spp. was reviewed by Kloepper et al. (2004). They detail the induction of resistance in various plant species against pathogens of various systematic groups. ISR elicited by *Bacillus* spp. was dependent on salicylic acid and also achieved plant growth promotion for transplanted vegetables (Kloepper et al. 2004). Similarly, *Pseudomonas fluorescens*, a plant growth promoting bacterial isolate triggers plant-mediated ISR response that is effective against a broad spectrum of plant pathogens (Pieterse et al. 2003).

Among natural disease control alternatives, our recent work has identified melanoidins (M), the macromolecular, nitrogenous end products of the non-enzymatic Maillard reaction, as potent inducers of plant immunity and growth (Elad et al. 2026a). We also demonstrated that M functions as a remarkably broad-spectrum inducer, effective against diverse necrotrophic pathogens, such as *Botrytis cinerea*, *Sclerotinia sclerotiorum*, and *Rhizoctonia solani*, as well as biotrophic pathogens like *Oidium neolycopersici* and *Blumeria graminis* (Elad et al. 2026b). This resistance is systemic and has been validated across a wide range of host plants, including eudicots like tomato, cucumber, and sweet basil, and monocots such as wheat.

Our previous work has shown that the mechanism of M-mediated disease resistance is primarily centered on the Salicylic Acid (SA) pathway, consistent with the induction of Systemic Acquired Resistance (SAR) (Elad et al. 2026a). Transcriptomic profiling reveals that M acts as a priming agent; it triggers a swift and transient upregulation of defense-related genes, allowing the plant to maintain a high state of immune readiness without the permanent metabolic burden of constitutive defense activation. M also promoted growth when used at low concentrations in the irrigation water

of a determinant tomato cultivar (Elad et al. 2026a). In that study, M was chemically characterized, and its biological activity was associated with the high-molecular-weight (>3 kDa) melanoidin fraction: the dia-filtered >3 kDa fraction retained the full activity of M, whereas the <3 kDa fraction, which contains the unreacted precursors and low-molecular-weight Maillard intermediates such as Amadori compounds, and the precursors glucose and glutamic acid themselves, were inactive in disease assays. Likewise, glucose and glutamic acid, alone or combined, did not promote tomato growth, whereas M did (Elad et al. 2026a, Fig. S2).

The growth-defense trade-off, where the redirection of energy toward immunity typically limits developmental processes, can present a barrier in agricultural productivity. Similar to the action of well-studied biocontrol agents like *Trichoderma* spp, which can stimulate growth even while inducing resistance, M appears to uncouple this trade-off and allow for simultaneous immunity activation and growth promotion. Our previous transcriptomic data shows that while M-treated plants may temporarily downregulate energy acquisition pathways like photosynthesis, they simultaneously upregulate genes associated with organ differentiation and growth (Elad et al. 2026a).

In the present study, we expand the scope of M's utility as a growth promoter. Following our report on increased growth in determinate tomato cultivars (Elad et al. 2026a), we examine the growth-promotive effects of M on an indeterminate tomato cultivar, as well as lettuce, sweet basil, cucumber, and wheat, revealing increased vegetative and reproductive plant's growth. Furthermore, given the known role of SA and beneficial microbes in mitigating environmental stress, we investigate the potential for M to assist plants in withstanding drought conditions. Beyond our earlier report, which was limited to a determinate tomato cultivar, the present study asks whether M-mediated growth promotion is general across eudicot and monocot species, whether it extends to reproductive traits and yield under commercial-like conditions, and whether it confers a benefit under abiotic (drought) stress.

Materials and Methods

Plant growth

Plants were grown in pots containing a potting mixture composed of peat and tuff (7:3 v/v, unsorted to 8 mm). One, 3 and 10-L plastic pots, were used in most experimental setups for growing the plants as earlier described (Elad et al. 2010, 2026ab, Graber et al. 2010, Gupta et al. 2021, 2022ab). Two-liter pots were used for drought experiments where perlite was used as a substrate. The perlite (medium size, 1.2 mm, Agrifusia, Fertilizers & Chemicals Ltd., Haifa, Israel) was washed in water prior to use and used as described earlier (Barnea et al. 2022, Elad et al. 2021a). The plants were grown and maintained in experimental net houses with no disease or pest challenge (Volcani Institute, Rishon LeZion, Israel). Fertigation was applied 2–3 times daily via a drip system with a 5:3:8 NPK fertilizer solution (Deshen Gat, Kiryat Gat, Israel), formulated to provide 120 mg L^{-1} nitrogen, 30 mg L^{-1} phosphorus, and 150 mg L^{-1} potassium (EC 2.2 dS/m), allowing for 25–40% drainage as detailed earlier (Elad et al. 2010, 2026ab, Graber et al. 2010, Gupta et al. 2021, 2022ab). The conditions during plants' growth and most experimental setups were as follows: temperatures between 19 and 27°C, RH>65% and daylight duration of 10 to 14 h. Specifics concerning experiments with different conditions are detailed below. The experiments were performed at Volcani Institute in Rishon LeZion (31°58'00.9" N 34°48'00.2" E). All plants were fertilized with the NPK fertilizer starting from seeding in the nursery and in the Volcani Institute greenhouses.

Plant species used in the research

Tomato (*Solanum lycopersicum*) plantlets of cultivar Ikram (Zeraim Gedera and Syngenta Vegetable Seeds, Israel) were obtained from Hishtil Nurseries (Ashkelon, Israel) 4-6 weeks after seeding. Cv. Ikram is a common indeterminate tomato variety. Seedlings were transplanted into 2

and 3L pots and grown for 4 to 6 weeks (Kumar et al. 2024) until used in experiments. Commercial-like experiments were conducted with greenhouse tomato plants grown in 10 L containers and maintained about 3 months after transplanting of the plantlets (Gupta et al. 2024). Plants were treated in the greenhouse weekly during the course of the experiments unless otherwise specified.

Lettuce (*Lactuca sativa*) cv. Raviv (Hazera Seeds, Shikmim, Israel) was transplanted into 1 L pots using seedling plugs after 6 weeks growth in the nursery (Hishtil, Nurseries, Kefar Yedidia, Israel). Lettuce leaves were initially treated 20 days after transplanting.

Sweet basil (*Ocimum basilicum*) cv. Peri (Agricultural Research Organization, Israel; Elad et al. 2017, 2021b) was used for all our experiments. The seedlings were grown in a commercial nursery (Shorashim, Mivtahim, Israel) and transplanted for the experiments 3 to 4 weeks after seeding in the nursery. Plugs of sweet basil seedlings were used, each containing three to five plants; hereafter, one plug is referred to as a "plant" as is common practice among growers and researchers (Elad et al. 2017, 2021b). Plants were transplanted into 1L pots and grown for 3 to 4 weeks until used in experiments.

Cucumber (*Cucumis sativus*) cv. Manny (Genesis Seeds, Israel) was seeded in the growth medium (Jaiswal et al. 2014). To prevent *Pythium* spp. related damping off, the medium was drenched once with a fungicide (0.25% Dynon in water drench, containing 722 g/L Propamocarb HCl, Bayer, Germany). Short-term experiments were carried out in 1 L pots and for long-term experiments, one cucumber plant was grown in each 3 L pots for 12 weeks (Elad et al. 2021a).

Wheat (*Triticum aestivum*) was grown in 3 L pots seeded with 6 seeds each, thinned to 5 seedlings/pot and grown for 7 to 13 weeks, cv. Bet Hashita (Hazera (1939) Ltd. Israel), was used throughout the experiments.

M synthesis and application

The *melanoidins* were synthesized by means of Maillard reaction in a dry synthesis method (8.5 min at 150°C) using L-glutamic acid and D-glucose. Powders of the ingredients were mixed with each other at an equimolar ratio and ground together as described recently (Elad et al. 2026ab). The resulting reaction product (M) consists of a high-molecular-weight melanoidin fraction together with low-molecular-weight Maillard reaction products and residual precursors; its characterization is summarized below (Elad et al. 2026a). The M powder was ground, placed in hermetically sealed vials, and kept in a desiccator with silica gel at room temperature until used (Elad et al. 2026). Plants were sprayed or drenched with M water solution at concentrations of 0.01, 0.03 and 0.1% as detailed in the results section. Spray applications were performed using a 1 L hand sprayer calibrated to emission of fine droplets until full canopy coverage was achieved. The solution was applied at volume of 8–15 mL per each mature plant depending on plant size. Drench applications consisted of 10–30 mL per pot, covering the volume of root zone with ~5% drainage (Elad et al. 2026). Fresh aqueous solutions of M were prepared immediately before each application. M was applied separately from the fertigation solution.

Characterization of M

M used in this study was produced by the same procedure as, and characterized in detail in, Elad et al. (2026ab). In brief, M contains 47.3% C and 6.1% N (elemental analysis). Serial ultrafiltration (100, 50, 30, 10, 5 and 3 kDa cut-offs) yielded only two size fractions: Fraction 1 (<3 kDa; 77.9% of the recovered material) and Fraction 2 (30–50 kDa; 22.1%). Residual (unreacted) glucose and glutamic acid, quantified by GC/MS after derivatization, together made up 15% of M. UV/Vis spectra of M and both fractions showed an absorbance peak at 285 nm, typical of Maillard intermediates such as Amadori compounds, di-carbonyls and furans, whereas absorbance at 405–420 nm, which operationally defines melanoidins, was highest in M and Fraction 2. M is highly water soluble (>100 g L^{-1} at 25 °C). Importantly, the diafiltered >3 kDa fraction, which is free of

unreacted precursors, retained the full biological activity of M, whereas the <3 kDa fraction and the precursors glucose and glutamic acid applied at 0.015% were inactive against B. cinerea, and the precursors, alone or combined, also did not promote tomato growth (Elad et al. 2026a, Fig. S2D–G). pH of the M 0.03 – 0.1% solution was ranged between 5.5 to 6.5. Because melanoidins are inherently heterogeneous polymers without a single defined structure (Morales et al. 2012), we refer to the whole reaction product as M throughout and report its activity for this defined preparation.

We used the entire Maillard reaction product as a whole for evaluating the effect of M on plants' growth. The residual starting materials, L-glutamic acid and D-glucose, together constitute 15% of M (Elad et al., 2026a). Consequently, L-glutamic acid and D-glucose were each applied at a final concentration of 0.015%, i.e., together twice the total residual precursor concentration in a 0.1% M solution. Spray of the two compounds either alone or in combination did not affect growth as demonstrated for tomato growth (see Elad et al. 2026a, Fig. S2F–G). Control plants were treated with an equal volume of water, applied by spray or drench as for the corresponding M treatment, in all experiments and no additives were supplemented to the M solution.

Effect of M on plants' growth

Tomato

To study the effect of drench and spray of M (0.03% and 0.1%) on the growth of tomato cv. Ikram, the plants were transplanted into 10 L containers, maintained under commercial-like conditions using the irrigation and fertilization as specified above, and supported in a vertical position by training on a 2.5 m long bamboo stick. The plants were treated with the experimental treatments once per week, at days 7, 14, 21, 28, 35, 42, and 49 after planting. The measured **vegetative** growth parameters were (a.) plant height at days 7 and 52; (b.) number of plant nodes at days 26 and 52; (c.) leaf no. 7 length at days 11 and 20; and (d.) terminal leaflet length (L) and width (W) at days 11

and 20, which were used to calculate leaflet area as LxW. The percent change in the four growth parameters was calculated as:

$$\%\ Change = \frac{(F - I)}{I} \times 100$$

where I is the initial measurement and F is the final measurement.

Reproductive parameters were (a.) number of inflorescences on each plant counted on day 52; (b.) the number of set fruits per plant at day 52; (c.) the ratio of mature (red) fruits at day 64; (d.) the weight of harvested fruits at day 64; and (e.) the calculated weight of a single fruit at day 64. The incidence of blossom end rot (f) was evaluated according to the ratio (in %) of the observed fruits having rot. There were 5 replicates in the tomato plant growth experiments.

Lettuce

Plants transplanted into 1 L pots were grown for two weeks and then treatments were applied twice, at days 0 and 3 of the experiments. Same age leaves were selected and marked. Leaf width (W) and length (L) dimensions were measured on days 10 and 15 after the initiation of the treatments, and the leaf area (W x L) at both dates were calculated. Change in leaf area in percent out of the initial area was calculated as a measure of growth during the evaluation period. There were 5 replicates in the lettuce plant growth experiments.

Sweet basil

Plants transplanted into 1 L pots were grown for two weeks, after which treatments were applied three times at weekly intervals. The fifth leaf on a sympodial branch was selected and marked in each pot. Leaf width and length dimensions were measured on days 13 and 21 after the initiation of the treatments, and the leaf area at both dates was calculated. Change in leaf area in percent out of the initial area was calculated as a measure of growth during the evaluation period. There were 5 replicates in the sweet basil plant growth experiments.

Cucumber

Plants seeded in 1 L pots were treated on a weekly basis, i.e. at days 7, 14 and 21 after seeding. Width and length dimensions of the 1st and 2nd formed true leaves were evaluated at days 21 and 27, respectively. The number of true leaves on each plant was evaluated at day 27 after seeding. In another set of experiments, cucumber plants grown in 3 L pots were treated on a weekly basis until day 28. The dimensions of leaf 8 were measured and the area was calculated at days 26 and 33, and the change in leaf area was calculated as a measure of its growth during that period. There were 6 replicates in the cucumber growth experiments.

Wheat

Starting from 13 days after sowing, all pots harbored 5 plants (see above). M applications started two weeks after seeding and were carried out once a week, i.e. 14, 21, 28, 35, 42, 49, 56, 63, 70, 77, and 84 days after seeding. The evaluated growth parameters were the number of tillers (side shoots) at day 55 after seeding, and number of spikes (heads) at days 62 and 93. There were 10 replicates in the wheat growth experiments.

Drought stress in tomato plants

Tomato plants cv. Ikram were grown in 2 L pots filled with perlite and fertigated as mentioned above. Plants were treated with M 21, 28, 35 and 42 days after transplanting. M concentrations used were 0.01 and 0.1%. Following the fourth application of M at day 42, the fertigation was stopped, water was let drain from the pots, and the pot containing the roots was placed in a polyethylene bag while the canopy was exposed to air. The plants were placed in a 23±1°C and 60 to 85% RH airconditioned walk-in, 14h-illuminated growth room (Jacob et al. 2008). The plants were kept for

21 days with no irrigation or fertigation and the weight, vegetative growth and wilt intensity of each of the plants and pots were measured individually. Weight of the plants including pots was measured every 3 to 4 days and the ratio of lost weight as compared with the initial weight at day 0 was calculated. The leaf length and the terminal leaflet area were measured at day 0 of the irrigation/fertigation end and at days 14 and 19, respectively. The wilt symptoms were evaluated 19 and 21 days after the stop of irrigation/fertigation on a 0–100% scale where 0=no wilt observed and 100=plants totally wilted. At the end of the 21-day drought conditions, the plants were irrigated and 14 hours later the number of leaves that did not recover from the wilting conditions were regarded as dead and were counted on each plant. There were 10 replicates in the drought experiments.

Data analysis

Experiments included 5 to 10 biological replicates for each treatment, as mentioned above specifically for each plant species, and all experiments were repeated twice. All data from both experiments are graphed. Data in percentages were arcsine-transformed before further analysis. Standard errors (SE) of the means were calculated considering the degrees of freedom (DF = n – 1), as described in previous publications (Elad et al. 2010; 2017; 2021ab; Rav David et al. 2019). The data were analyzed using ANOVA and the Tukey–Kramer HSD test. Statistical analysis was performed ($\alpha = 5\%$) using JMP software (SAS Institute, Cary, NC, USA). Values of each parameter followed by a different letter are significantly different from each other.

Results

We recently demonstrated that M increased tomato plants' growth when applied continuously in a low concentration as part of every fertigation, or when given at a series of 4 weekly intervals (Elad

et al. 2026a). To further test the effect of M on the vegetative growth and reproduction in eudicot and monocot plant species, we used an indeterminate tomato cultivar, and plants of lettuce, sweet basil, cucumber and wheat.

Promotion of growth and reproduction in tomato plants

Tomato plants were grown for 52 days after transplanting and treated seven times, once every week from day 7 until day 49, with 0.03 and 0.1% M drench and/or spray. Significant increase in plants' height was obtained by the two 0.1% spray and drench treatments and not by the 0.03% treatments (Fig. 1A). Significant increase in the number of formed nodes was obtained by three of the four treatments and not by 0.03% spray (Fig. 1B). Similarly, significant increase in leaf length (Fig. 1C) and leaflet area (Fig. 1D) was obtained by the same three treatments and not by 0.03% spray.

The number of inflorescences was significantly increased only by the 0.03% M spray treatments (Fig. 2A), but all four treatments significantly increased the number of fruits, while the 0.1% M spray was less effective as compared with the other M treatments (Fig. 2B). The 0.1% M drench and spray treatments increased the ratio of red fruits out of all, red and green fruits (Fig. 2C). All treatments but 0.03% M spray significantly increased the total fruit weight by the end of the growth cycle (Fig. 2D) and the weight of a single fruit was increased by all M treatments except for the 0.1% M spray (Fig. 2E). Blossom end rot incidence on mature fruits reached 15.8% of the fruits of the untreated control plants and all treatments significantly reduced its incidence (Fig. 2F).

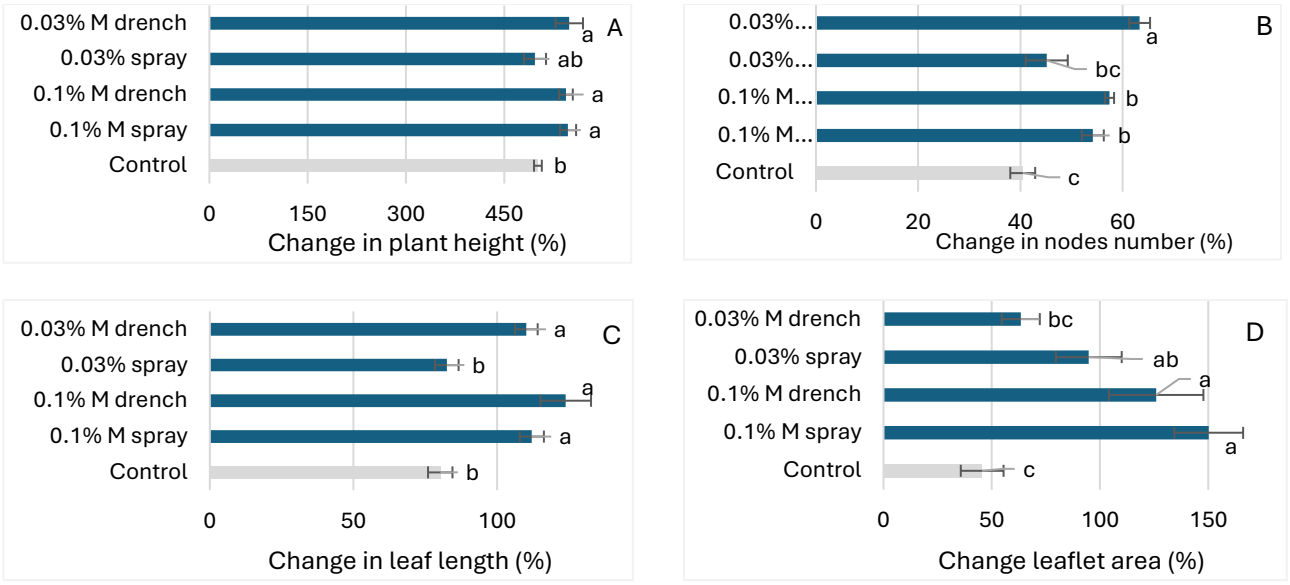


Fig. 1 Effect on vegetative growth parameters of drench and spray of M at concentrations of 0.03% and 0.1% applied weekly from 7 to 49 days after planting to tomato plants cv. Ikram. (A.) Change in the height of plants measured on day 52 after planting as compared with plant height at day 7. (B.) Change in the number of plant nodes counted on day 52 after planting, as compared with the number at day 26. (C.) Change in the length of leaf no. 7 measured on day 20 after planting as compared with leaf length at day 11. (D.) Change in terminal leaflet area of leaf 7 measured on day 20 after planting as compared with leaflet area at day 11. In each graph, values followed by a different letter are significantly different according to one-way ANOVA with Tukey–Kramer's HSD test. Default significance levels were set at $\alpha = 0.05$. Bars = SEs, n=5.

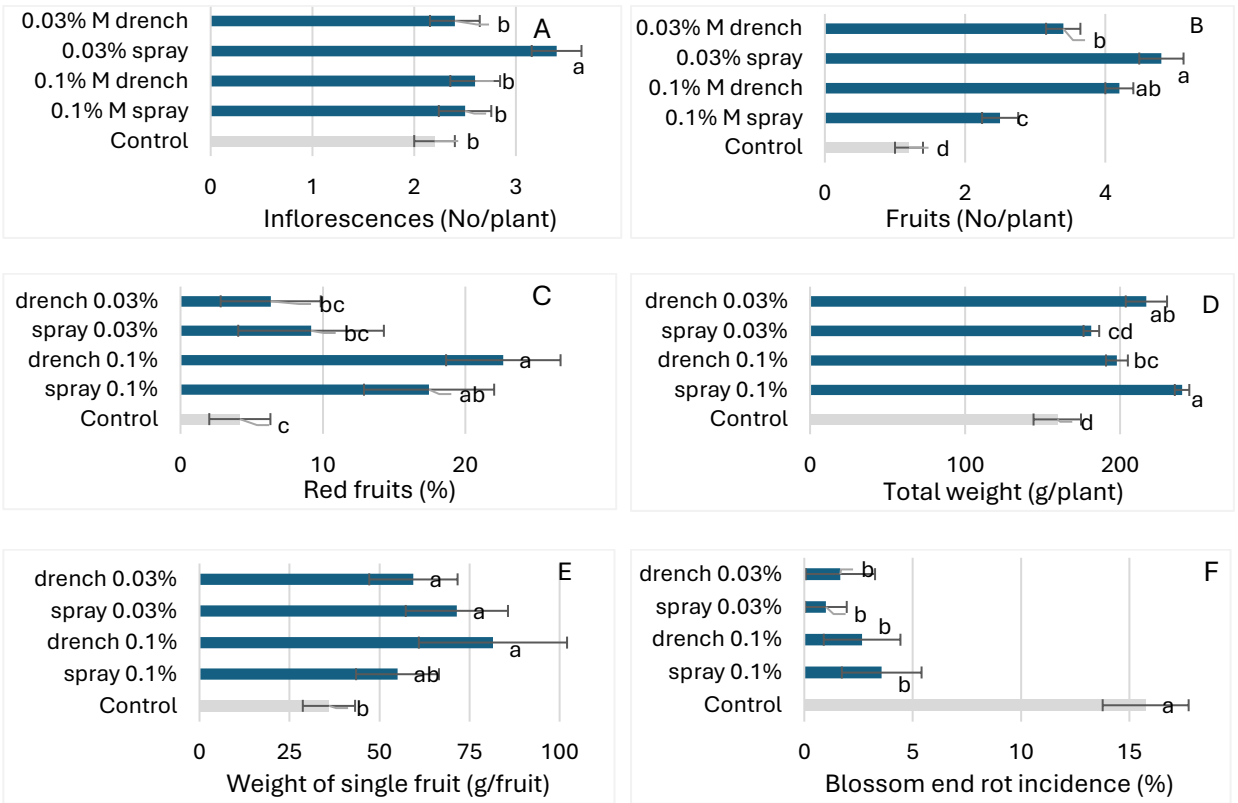


Fig. 2 Effect on reproductive parameters of drench and spray of M at concentrations of 0.03% and 0.1% applied to tomato plants cv. Ikram on a weekly basis from 7 until 49 days after planting. (A.) The number of inflorescences at day 52 after planting. (B.) The number of set fruits at day 52 after planting. (C.) Ratio of red fruits out of all harvested fruits at day 64. (D.) Weight of harvested fruits at date 64. (E.) Weight of a single fruit at day 64. (F.) Ratio of fruits bearing blossom end rot at day 64. In each graph, values followed by a different letter are significantly different according to one-way ANOVA with Tukey–Kramer's HSD test. Default significance levels were set at $\alpha = 0.05$. Bars = SEs, n=5.

M promotes lettuce and sweet basil growth

In lettuce the 0.03% M spray and drench and 0.1% M spray significantly increased the leaf size while 0.1% drench was significantly similar to all treatments and to the untreated control (Fig. 3A) and in sweet basil both the 0.01 and 0.1% M spray and drench treatments significantly increased the leaf size (Fig. 3B).

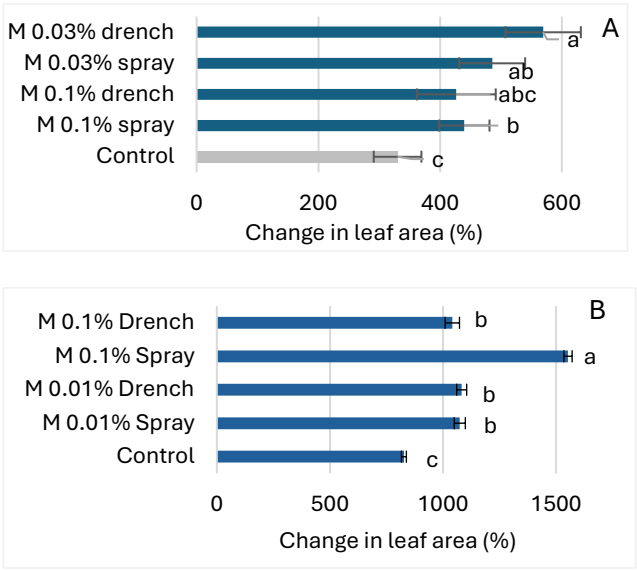


Fig. 3 Effect of M on leaf size of lettuce (A) and sweet basil (B). (A.) Effect of spray and drench of 0.03- and 0.1%- M, applied twice at days 0 and 3 on lettuce leaf area measured at days 10 and 15. The ratio of increase of measured leaf area between the two measurements is presented. (B**.)** Effect of spray and drench of 0.01 and 0.1% M, applied three times at weekly intervals, on leaf area measured at days 13 and 21. The increase of measured leaf area between the two measurements is presented. Values followed by a different letter are significantly different according to one-way ANOVA with Tukey–Kramer's HSD test. Default significance levels were set at $\alpha = 0.05$. Bars = SEs, n=5.

Effect of M on cucumber leaf development

The size of the first and second true (secondary) leaves was measured at 21 and 27 days after seeding, respectively, and the number of true leaves were all significantly increased by M 0.03 and 0.01% spray treatments (Fig. 4A-C). The change in the size of the eighth leaf during days 26 to 33 was significantly higher in M 0.03 and 0.1% spray and drench treatments than in the control (Fig. 4D).

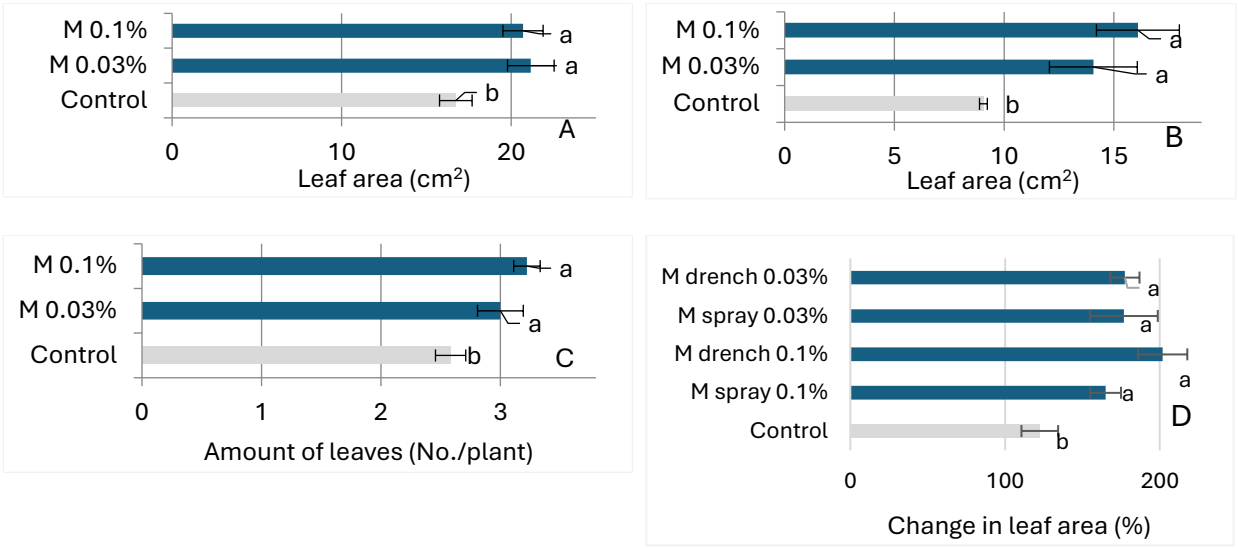


Fig. 4 A-C. Effect of spray of M at concentrations of 0.03 and 0.1% at 7, 14 and 21 days after seeding on cucumber true leaves development. (A.) Size of 1st true leaf at 21 days after seeding. (B.) Size of the 2nd true leaf at 27 days after seeding, and (C.) Number of the developed true leaves at 27 days after seeding. D. Effect of M spray and drench at concentrations of 0.03 and 0.1% applied at 7, 14, 21 and 28 days after treatments initiation on the size change in leaf 8 area from day 26 to day 33. Values followed by a different letter are significantly different according to one-way ANOVA with Tukey–Kramer's HSD test. Default significance levels were set at $\alpha = 0.05$. Bars = SEs, n=6.

M promotes formation of tillers and spikes' development in wheat

To test the growth promoting effects of M on a monocot plant species, wheat was grown for 93 days after seeding and treated for 11 consecutive weeks by drenching and by spraying M at concentrations of 0.03 and 0.1% (Fig. 5). The number of tillers formed by the wheat plants was significantly

increased by all treatments (Fig. 5A). The number of spikes 62 days after seeding was increased by the 0.1% M treatments and by 0.03% spray treatment (Fig. 5B). The number of spikes counted at 93 days was not increased by the 0.03% spray treatment, and it was increased by the other three treatments, yet the 0.03% drench treatment accumulated more spikes than the 0.1% drench and spray treatments (Fig. 5B).

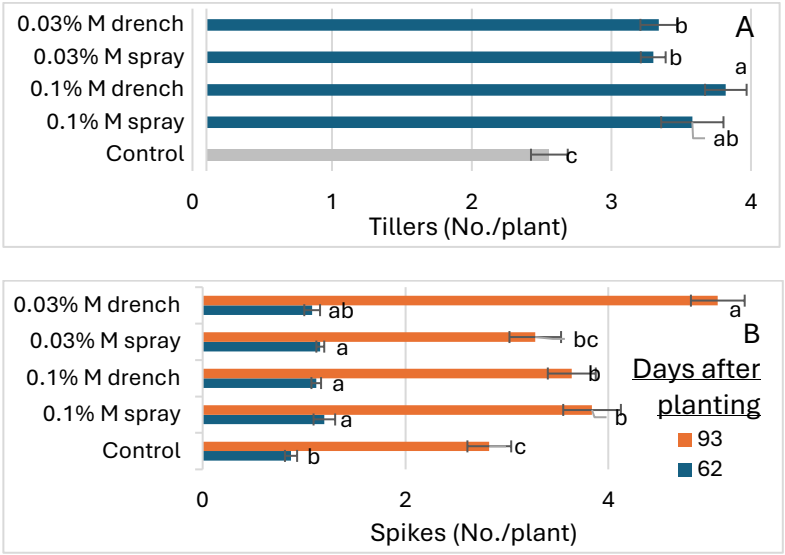


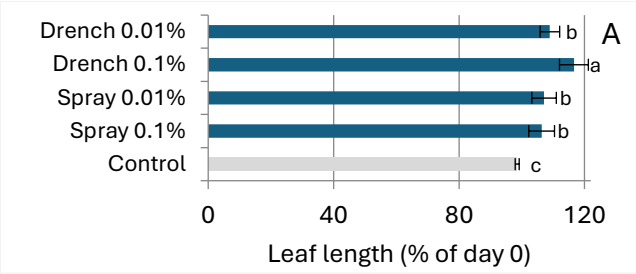
Fig. 5 Effect on growth parameters of drench and spray of M (0.03% and 0.1%) applied to wheat plants cv. Bet Hashita on a weekly basis from 14 until 84 days after planting. (A.) Formation of tillers by the wheat plants at day 55 after seeding. (B.) The number of spikes as was counted at two sampling dates. In each graph and date, values followed by a different letter are significantly different according to one-way ANOVA with Tukey–Kramer's HSD test. Default significance levels were set at $\alpha = 0.05$. Bars = SEs, n=10.

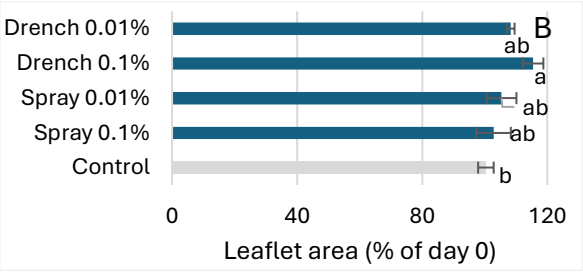
M alleviates drought stress in tomato

Tomato plants grown in perlite were sprayed and drenched with M 0.01 and 0.1% starting at 21 days after transplanting and ending at day 21 after treatment initiation. Following the three weeks of treatments and fertigation, irrigation and fertigation were ceased. The fertigation and treatments of the plants were stopped at day 0 of the drought stress implementation and then the plants were monitored for vegetative growth parameters and wilt severity until 21 days after end of

irrigation/fertigation. At 15 days with no irrigation the loss of weight slowed drastically and at 21 it was maximal, reaching 31.6% of the initial weight of the control plants. A significant lower weight loss was observed for the M treated plants, reaching 37.1 and 37.2% weight compared to the weight at day 0, in the 0.01 and 0.1% M spray-treated plants, respectively, and 36.0 and 38.1% weight compared to the weight at day 0, in the respective 0.01 and 0.1% M drench-treated plants.

To test if the plants continued growing, the leaf length and leaflet area were measured (Figs. 6 A and B). Vegetative growth parameters were followed to test if the plants continued their growth in spite of the drought conditions. The increase in length of leaves was significantly larger in the plants treated with each of the four M treatments, revealing continuous growth during the drought conditions (Fig. 6A) and the increase in leaflet area was significant for the 0.1% drench treatment, meaning a continuation of growth for this treatment (Fig. 6B). At day 19 after irrigation cessation, the wilt severity of plants in the M 0.1% drench and spray treatments was significantly lower than in the 0.01% treatments. At day 21, the severity of wilt was significantly lower in the 0.01% spray treatment and the two concentration drench treatments (Fig. 6C). The plants were irrigated following the wilt evaluation at day 21 of drought, and part of the leaves in each plant were revived after the rewatering. The number of revived leaves was significantly higher in each of the M treatments (Fig. 6D). Drought affected plants from the control and drench treatments are presented (Fig. 6).





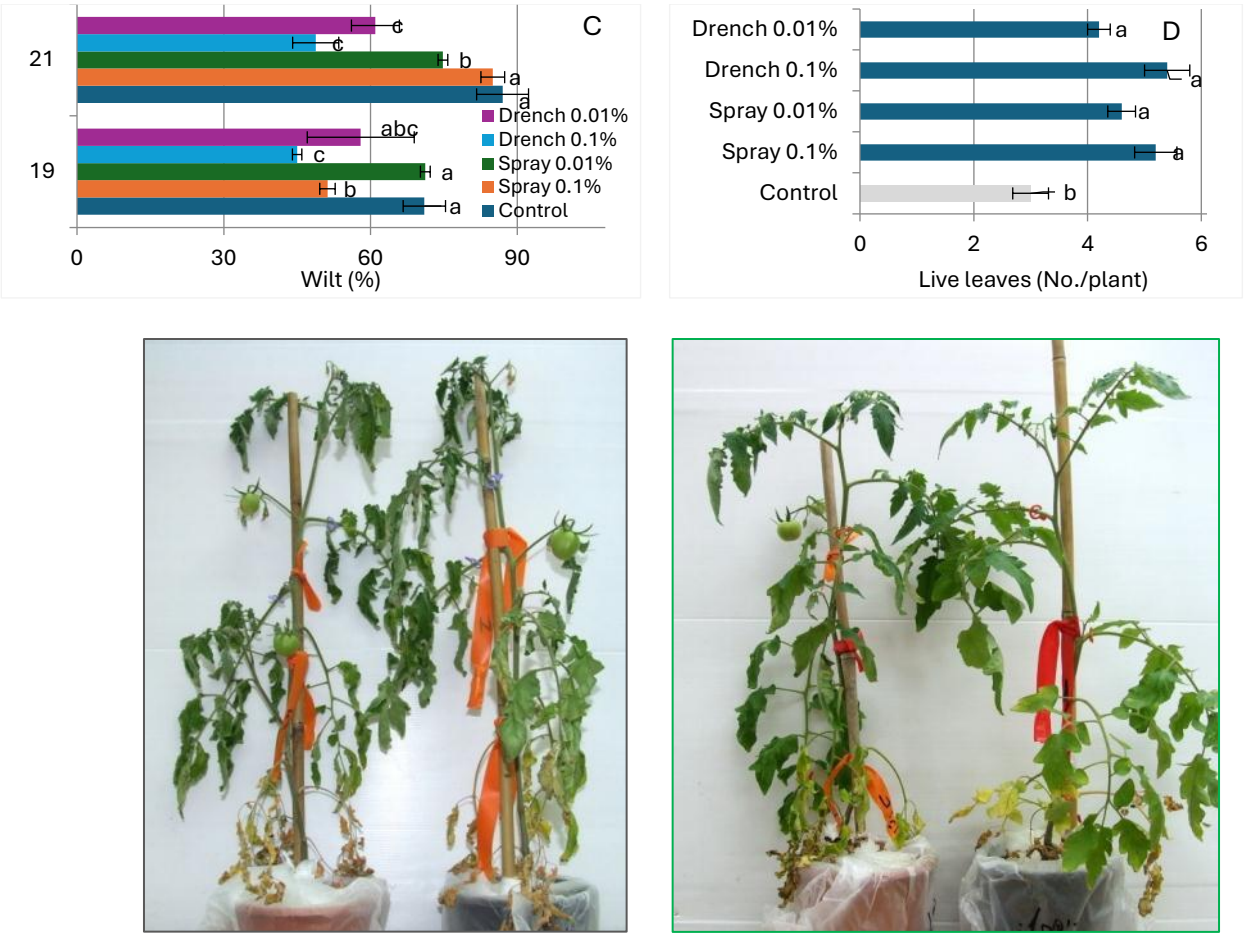


Fig. 6. Drought stress in tomato plants cv. Ikram. Following four weekly applications of M by drench and spray at concentrations of 0.01 and 0.1%, the fertigation was stopped, and growth and wilt parameters were followed for 21 days. (A.) Change in leaf length during the period of 14 days after fertigation stop (day 0). (B.) Change in the leaflet area from the initial day of no fertigation until day 9 of the drought period. (C.) Severity of the wilt of the tomato plants at days 19 and 21 after end of the fertigation. (D.) Rewetting of the plants was carried out at the end of day 21 and the number of dead leaves in the tomato plants was evaluated 14 h after the rewetting. In each graph and date, values followed by a different letter are significantly different according to one-way ANOVA with Tukey–Kramer's HSD test. Default significance levels were set at $\alpha = 0.05$. Bars = SEs, n=10. Images at the bottom row present plants from the control (left) and M 0.1% drench (right) treatments.

Discussion

A persistent challenge in plant biology and agriculture is the trade-off between plant growth and pathogen defense, where the energetic costs of defense may typically limit development (Ku et al. 2024). Our present results show that M-mediated immunity does not carry this penalty. Expanding on our previous work (Elad et al. 2026a), we show here that M treatment promoted vegetative and

reproductive growth. Weekly applications of M either as drench or as spray increased the vegetative growth of tomato plants and the reproductive phase of these plants with the result of a larger canopy area and more fruits; most of the M treatments increased plant height, number of nodes, leaf length and leaflet area in an indeterminate tomato cultivar (Fig. 1). Most of the M treatments also promoted the reproductive parameters of amount of set fruits, the ratio of red fruits out of all fruits, total fruit weight and the weight of a single tomato fruit in plants grown under commercial-like conditions (Fig. 2). Increased growth response in tomato plants is quite common among biocontrol agents (Romero et al. 2016; Windham et al. 1986). Biological agents like *Trichoderma* spp., *Bacillus* spp., and *Pseudomonas* spp. are well-known "twin service providers" that simultaneously enhance both plant growth and immunity (Gupta et al. 2020). For example, *T. harzianum* T39 and *B. megaterium* 4C have been shown to promote several developmental and agricultural traits in tomato while maintaining robust resistance (Leibman-Markus et al. 2023). These biologicals often function through nutrient solubilization and the production of phytohormones like auxins, gibberellins, and cytokinins, which improve root architecture and shoot development (Gupta et al. 2020).

Blossom end rot is a severe physiological disorder in tomato fruits (Hagassou et al. 2019), attributed to a reduced root uptake and an aberrant regulation of cellular partitioning of calcium as the major agent. It is also hypothesized that it may be a result of abiotic stresses, which may lead to membrane disintegration and loss of cell turgor through the response to increased accumulation of oxygen radicals (Hagassou et al. 2019). Interestingly, M drench and spray treatments reduced the incidence of blossom end rot in the tomato fruits (Fig. 2F). Similarly, ASM, found to induce systemic acquired resistance (SAR), reduced blossom end rot in tomato fruits (Fanigliulo et al. 2015; Giuliani et al. 2014). Giuliani et al. (2014) correlated this phenomenon with the fact that treated plants were more resistant to water stress.

We observed positive effects of M treatment on several crops. Increases in leaf size were observed in tomato (Fig. 1C-D), lettuce (Fig. 3A), and sweet basil (Fig. 3B). M increased the number of true

leaves and leaves' size in young cucumber plants, and the leaf size in plants grown for 33 days (Fig. 4). Similarly, increase in lettuce plant weight was induced by some biocontrol fungi and bacteria and by ASM (Abada et al. 2017). Likewise, the weight and height of the sweet basil both significantly increased following treatment with the elicitor chitosan (Kim et al. 2005)

In wheat grown for 3 months, M treatments increased the numbers of produced tillers and spikes (Fig. 5). Wheat, being a monocot, is reported to be affected by resistance inducers that result in the reduction of various diseases (Kashyap et al. 2021; Görlach et al. 1996) but to our knowledge, with the exception of PGPR mediated growth promotion, the effect on wheat growth by such inducers in the absence of plant diseases was not reported, and in fact, the effect of resistance inducers on wheat was rarely investigated until our recent findings regarding M's efficacy in monocots (Elad et al. 2026b).

These effects on plants growth were obtained in the absence of disease. Gupta and Bar (2020) previously reported that inducers of resistance can promote plant growth. Chemical and biological immunity inducers can promote induced disease resistance in the same pathway that they promote plant growth (Leibman-Markus et al. 2023). For instance, ASM (Bion; Ishii et al. 2019), and the above-mentioned *T. harzianum* T39, that activates ISR (Meller Harel et al. 2014; Perrazzolli et al. 2008), promote disease resistance and growth in the same respective pathways (Leibman-Markus et al. 2023). Interestingly, while ASM is often associated with energy costs that result in growth penalties at higher doses, very low concentrations (0.001%) have been found to promote vertical growth in tomato without metabolic penalties (Leibman-Markus et al. 2023). Similarly, certain strobilurins like Pyraclostrobin and the natural biopolymer Chitosan have been reported to improve plant health and yield even in the absence of disease pressure (Yassin et al. 2021; Chakraborty et al. 2020). Chitosan, in particular, mirrors M's performance, in that case- by accelerating root and shoot length through improved nutrient uptake and cell division (Chakraborty et al. 2020).

Thus, controlling disease with immunity inducers can have the added benefit of promoting growth pathways. For M, the uncoupling of growth and defense is supported by transcriptomic data showing that while M-treated plants temporarily downregulate energy acquisition (photosynthesis), they simultaneously upregulate genes associated with organ differentiation (Elad et al. 2026a). In this sense, M "encodes" for growth priming alongside immune priming, allowing the plant to maintain a high immune alert while promoting yield production. This uncoupling may be further influenced by M's interaction with leaf-stage associated immunity (Paper under review). Our research indicates that M provides uniform suppression across leaves of all ages, potentially supplementing or overriding natural developmental vulnerabilities, such as the lower salicylic acid (SA)/Jasmonic Acid (JA) ratios found in later-developing leaves. This activity might bolster immunity during the critical pre-flowering vegetative phase (Lindner et al. 2025; paper under review). Furthermore, while growth promotion is traditionally a hallmark of Induced Systemic Resistance (ISR) triggered by beneficial microbes, M achieves these effects through the SA pathway typically associated with Systemic Acquired Resistance (SAR) (Elad et al. 2026ab). This suggests that growth potentiation following immune activation may be a specific property of the M-host interaction rather than the ISR/SAR category.

To test whether M has a beneficial effect on plants during drought stress, fertigation of the tomato plants was stopped and during 3 weeks of no fertigation the continued growth of the plants was tested (Fig. 6). Leaves' growth following the M 0.01 and 0.1% drench and spray treatments was increased significantly more than the growth of the untreated leaves and 0.1% M drench significantly increased leaf size. (Fig. 6A, B), indicating continuation of plants growth during drought conditions. Additionally, most M treatments reduced wilt symptoms after 3 weeks (Fig. 6C) and following rewatering, significantly more leaves were alive in the revived plants treated by M (Fig. 6D). Thus, M mitigated the effects of drought stress in tomato plants. Because M-treated plants lost less plant and pot weight during the drought period than control plants, the protective effect can

be attributed to reduced water use by plants or from increased water retention in the substrate. Nevertheless, M-treated plants maintained growth while tolerating a lower water status; physiological measurements such as stomatal conductance and relative water content will be needed to resolve the underlying mechanism. Similarly, tomato plants treated with acibenzolar-S-methyl (ASM) were more resistant to water stress for a longer period than untreated ones (Fanigliulo et al. 2015; Giuliani et al. 2014). Similarly to the effect of M presented here and the effect of ASM on plants growth and resistance to water stress, both in tomato, Kordi et al. (2013) reported that salicylic acid caused increased sweet basil growth and decreased adverse effects of drought stress. The ability of M to mitigate drought aligns with reports of plant growth-promoting rhizobacteria (PGPR) like *Bacillus safensis*, which enhance water stress tolerance by improving antioxidant capacity and water use efficiency (Chakraborty et al. 2013). Certain *Trichoderma* strains also provide this benefit, helping plants tolerate abiotic stressors such as salinity and drought alongside their biocontrol functions (Gupta et al. 2020; Srivastava et al. 2026).

Conclusion

M treatments to plants resulted in increased growth response in eudicot and monocot plants. Tomato and wheat also showed improved reproductive traits. The increase in plant growth in tomato was also coupled with reduced effects of drought stress. These effects potentially present the M solution as not only an inducer of disease resistance (Elad et al. 2026ab) but also as a promoter of growth in various plant species under conditions with no visible stress. In tomato we report that M assists plants in coping with drought stress. Its high water solubility and ease of synthesis (Elad et al. 2026ab) position M as a robust candidate for sustainable agriculture and integrated disease (and perhaps also abiotic stress) management programs.

Author Contributions Yigal Elad: Writing – review & editing, writing – original draft, supervision, methodology, investigation, formal analysis, conceptualization. Ellen R. Graber: Writing – review & editing, supervision, methodology, investigation, funding acquisition, formal analysis, conceptualization. Dalia Rav-David: Methodology, investigation, formal analysis. Ludmila Tsechansky: methodology, Investigation. Maya Bar: Analysis, writing, reviewing and editing.

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Declaration The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ellen Ruth Graber, Dalia Rav-David, and Yigal Elad are inventors in a series of patents belonging to the families of PCT patent application No.s WO2020261273, entitled "Melanoidin compositions for protecting crops from nonfungal pests", and WO2014111932, entitled "Melanoidins and their use for improving properties of plants", which include data described in this paper.

Data Availability The authors declare that the data supporting the findings of this study are available within the paper and its Supporting Information files. Raw data is available from the corresponding author upon reasonable request.

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