



Enhancing host biochemical defence system against *Bipolaris maydis* through seed priming with maize (*Zea mays*) phyllosphere endophytic bacteria

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Received: 21 June 2024; Accepted: 12 December 2024

ABSTRACT

Maize (*Zea mays* L.) is an important cereal crop, significantly contributing to the global economy and advancing plant genetic research. One of the most serious diseases, maydis leaf blight (MLB), incited by *Bipolaris maydis*, reduces the yield and quality of maize. The present study was carried out during rainy (*kharif*) season (June–Oct) of 2022 and 2023 at ICAR-Indian Agriculture Research Institute, New Delhi to identify promising phyllosphere endophytic bacteria against *Bipolaris maydis* as an appropriate alternative to the traditional commercial fungicides, which also aligns with the goal of promoting sustainable and eco-friendly agriculture. Three different concentrations of phyllosphere endophytic bacteria, viz. *Stentrophomonas maltophilia*, *Brevundimonas olei* and *Pseudomonas aeruginosa* were investigated for MLB disease reduction and activation of maize biochemical defence system against *Bipolaris maydis* after seed priming. The recorded *in planta* percent disease index (PDI) data were analysed using a randomized block design (RBD) while all replications for biochemical assay were arranged in a completely randomized design (CRD) and subjected to the analysis of variance (ANOVA). Disease scoring in both seasons recorded the lowest PDI at the highest concentration of *Stentrophomonas maltophilia*, followed by *Brevundimonas olei* and *Pseudomonas aeruginosa*. Biochemical activities of phenylalanine ammonia-lyase (PAL), PR protein β -1,3-glucanase, and non-enzymatic antioxidant including total polyphenol with total sugar content were recorded for both inoculated and uninoculated set of treatments. In addition, seeds primed with the highest concentration 1.0 at OD₆₀₀ of *Stentrophomonas maltophilia* and *Brevundimonas olei* recorded elevated sugar levels, enzymatic as well as non-enzymatic activities after *Bipolaris maydis* inoculation. This study demonstrated that the changes in biochemical activities correspond with the developmental stages of the pathogen *Bipolaris maydis* which inhibited its growth. The biochemical defence activities varied differentially during disease progression on the host plant.

Keywords: Bacteria, Biochemical, Endophytes, Maize, Maydis leaf blight

Maize (*Zea mays* L.) is one of the vital cereal crops with a total cropping area of 197 Mha worldwide (Liu *et al.* 2023) and an average yield of 3.02 t/ha (FAO 2021). India occupies 4th position globally in terms of total maize cultivated area and 7th in production (Hamidi *et al.* 2024). As one of the economically most important crops, the yield is highly impacted by biotic and abiotic stresses. Southern corn leaf blight (SCLB) or maydis leaf blight (MLB), incited by *Bipolaris maydis* Shoemaker (Teleomorph *Cochliobolus heterostrophus* Drechs.) stands out as a major threat which is particularly prevalent in warm to humid, tropical to temperate regions of India. Under favourable conditions, this pathogen can completely devastate the crop resulting

100% yield loss. To manage MLB, several fungicides have proven effective while their residual toxicity and adverse impact on environment is always a threat to future generations. Therefore, biological control approaches are the new alternative to these harmful chemicals and the use of plant-associated beneficial microorganisms is gaining more attention.

The compatible interaction between plant and pathogen on its arrival can successfully establish disease. Due to high metabolic cost, most defence mechanisms are triggered after the pathogen attack. Plants have evolved an extensive array of enzymatic and non-enzymatic antioxidants to tightly regulate the levels of reactive oxygen species (ROS) in living cells, ensuring the maintenance of redox balance. Plant cells contain enzymes and antioxidants such as catalase, phenylalanine ammonia lyase (PAL), β -1,3-glucanase etc. Additionally, there are defence compounds like phenolics, flavonoids and tannins which contribute significantly towards ROS balancing in plant cell. While

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there is adequate information available on the contribution of inherent biochemical compounds in maize plant, our understanding of antioxidant defence and regulation defence compounds triggered by promising endophytic bacteria against MLB remains limited. In the present study, three promising endophytic phyllosphere bacteria such as *Stentrophomonas maltophilia*, *Brevundimonas olei* and *Pseudomonas aeruginosa* were used as seed priming agents to investigate the MLB incidence and activation of biochemical enzymes/non-enzymes against *Bipolaris maydis* on the susceptible maize variety CM 119.

MATERIALS AND METHODS

Morpho-molecular identification and maintenance of fungal pathogen: The present study was carried out during rainy (*khari*) season (June–Oct) of 2022 and 2023 at ICAR-Indian Agriculture Research Institute, New Delhi. The original culture of *Bipolaris maydis* was obtained from Maize Pathology Lab (ITCC Accession no. 6028), ICAR-Indian Agricultural Research Institute, New Delhi. The preserved culture was subsequently grown on potato dextrose agar (PDA) medium. The new mycelia and actively growing culture were inoculated into maize seedlings, to enhance the revival and aggressiveness through the host and the fungus was re-isolated on oat meal agar (OMA) medium for better sporulation. The spores were observed to confirm the pathogen. For reconfirmation, molecular based sequencing of a region of the nuclear rDNA gene was performed using ITS1 (5'TCCGTAGGTGAACCTGCG3') and ITS4 (5'CTCCGCTTATTGATATGCT3') primers. Sequence curation and contig assembly was carried out using Finch TV (<https://digitalworldbiology.com/FinchTV>) and CLC sequence viewer 8.0 (<https://clc-sequence-viewer.software.informer.com/8.0/>), respectively. Final sequence is compared with the other sequences through BLAST analysis in NCBI (<https://www.ncbi.nlm.nih.gov/search/>), and the identity was confirmed by the closest match. Generated sequences were submitted to NCBI to obtain the unique GenBank accession number. To know the genetic relationships between the fungi and other ITS sequences retrieved from NCBI, a phylogenetic tree was constructed by using the Maximum Likelihood method and Tamura-Nei model in MEGA11 software (Tamura *et al.* 2021). This analysis comprised 10 nucleotide sequences and the bootstrap consensus tree is derived from 1000 replicates, where branches corresponding to partitions reproduced in less than 50% bootstrap replicates were collapsed.

Isolation and identification of phyllosphere endophytic bacteria: Isolation of endophytic bacteria from resistant variety (var. SC-7) of maize leaf was carried out by following the standard isolation protocol as described by Kumar *et al.* (2021). To confirm the bacteria, molecular based identification through 16s rRNA gene amplification was followed with the standard procedure (Yang *et al.* 2008). Agarose gel purified PCR amplicon was further analysed using Sanger's dideoxy chain termination method to ensure accurate and precise coverage of the gene

sequence (Munjal *et al.* 2016). The final sequences were submitted in NCBI to get the unique GenBank accession number. The promising bacteria used in this study were *Stentrophomonas maltophilia* (GenBank Accession no: OR708535), *Brevundimonas olei* (GenBank Accession no: OR708528) and *Pseudomonas aeruginosa* (GenBank Accession no: OR708533).

In planta assay of endophytic bacteria for effectiveness against MLB: A plot size of 12 m × 10 m was prepared with a spacing of 0.7 m × 0.3 m (row × plant) containing 15 maize plants. A total of 12 treatments, viz. T₁ (*Stentrophomonas maltophilia*, conc. 0.01); T₂ (*Stentrophomonas maltophilia*, conc. 0.1); T₃ (*Stentrophomonas maltophilia*, conc. 1.0); T₄ (*Brevundimonas olei*, conc. 0.01); T₅ (*Brevundimonas olei* 0.1); T₆ (*Brevundimonas olei*, conc. 1.0); T₇ (*Pseudomonas aeruginosa*, conc. 0.01); T₈ (*Pseudomonas aeruginosa* conc. 0.1) and T₉ (*Pseudomonas aeruginosa* conc. 1.0) with three replications were studied in randomized block design (RBD); T₁₀ (negative control) with pathogen inoculation; T₁₁ (fungicidal control with Mancozeb 75% WP @2000 mg/L) as foliar spray and T₁₂ (absolute control) without pathogen inoculation and only water spray was maintained. The required numbers of seeds of susceptible maize variety (var. CM 119) were soaked overnight separately by inoculating the bacterial colonies of three different concentrations. For the treatment negative, fungicidal and absolute control, seeds were soaked in sterile distilled water. Whorl inoculation was carried out at 35 days after sowing (stage 5 of maize growth stages) with 5 g of *Bipolaris maydis* inoculum (Payak and Sharma 1983). Disease scoring for MLB was carried out two times at 10 days interval (20th and 30th DAI) for both the seasons as described by All India Co-ordinated Maize Improvement Project (Anonymous 2016) (Supplementary Table 1). Percentage disease index (PDI) was calculated by using the formula given by McKinney (1923):

$$PDI = \frac{\text{Sum of all numerical ratings}}{\frac{\text{Total number of plants observed} \times \text{Maximum grade of disease rating}}{}} \times 100$$

Collection of maize leaf samples for biochemical assay: Samples were collected aseptically at different time points (0, 24, 48, 72 and 96 h) with three replications for each treatment, transported to the laboratory in liquid nitrogen and finally stored at -80°C for further biochemical assays.

Analysis of biochemical constituents of maize

Total sugars: Fungal pathogens highly rely on the resources of host plant such as sugar for their growth and reproduction. Understanding sugar levels can help in studying pathogen infection strategies. Total sugar content was determined by anthrone method (Yemm and Willis 1954) with required modifications as described by Meshram *et al.* (2020). Absorbance was recorded at 625 nm before and after pathogen inoculation for all the treatments. The total sugar concentration was estimated by following standard glucose curve.

Analysis of enzymatic antioxidant of maize

β -1,3- glucanase assay: The β -1,3- glucanase activity was evaluated by incubating the enzyme extract with laminarin solution and the absorbance was measured at 500 nm after adding dinitro salicylic reagent to immediately stop the reaction (Dorjee *et al.* 2023).

$$y = 0.0004x$$

where y is the absorbance at 500 nm and x is the concentration.

Phenylalanine ammonia lyase (PAL) assay: The induction of PAL was measured as described by Meshram *et al.* (2020) with minor alteration adopted using L-phenylalanine as a substrate. The PAL activity was determined using trans-cinnamic standard curve. The absorbance was measured at 290nm using spectrophotometer (EPOCH L2 microplate reader, Agilent Technologies, USA).

$$y = 0.0008x + 0.0069$$

where y is the absorbance at 290 nm and x is the concentration calculated.

Analysis of non-enzymatic antioxidant of maize

Total polyphenols: The total polyphenol content was determined following the standard protocol (Sarker and Oba 2018). Total polyphenol was estimated using Folin-Ciocalteu (FC) reagent with gallic acid as a standard curve (Ashajyothi *et al.* 2023). The equation for the assay is as follows:

$$TPC = \frac{[F(S) - I(S) F(B) - I(B)]}{0.01xt}$$

where F(S) and F(B), Final absorption values of sample and blank; I(S) and I(B), Initial absorption values of sample and blank.

Statistical analysis: All the experiments in this study were repeated twice. The recorded *in planta* PDI data were analysed using a randomized block design (RBD) while all replications for biochemical assay were arranged in a completely randomized design (CRD) and subjected to the analysis of variance (ANOVA). Statistical analysis

was performed on all replicated samples using SPSS version 16. The outcomes were expressed as the mean of three replications. Duncan's multiple range test was used to compare treatment mean values at a significance level $P \leq 0.05$.

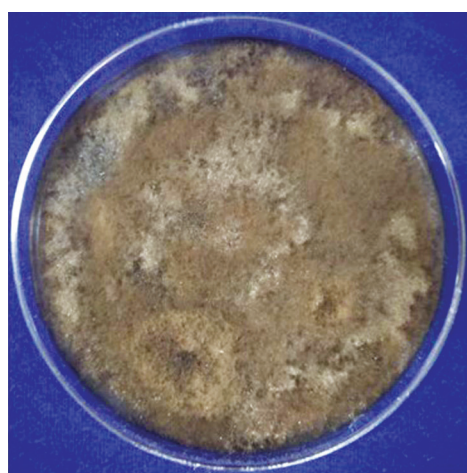
RESULTS AND DISCUSSIONS

Morpho-molecular identification: The fungal pathogen *Bipolaris maydis* was grown on OMA medium for better sporulation of the fungus. On this medium, the mycelia appeared black to brown in colour with less cottony growth. The fungal spores were observed under microscope where distinct brown-coloured conidia with pseudosepta were seen (Fig. 1). The size of the conidia was measured in the range of $51\text{--}67 \mu\text{m} \times 11\text{--}16 \mu\text{m}$ (length $\times$ width) exhibiting a banana shaped slightly curved appearance, which is the distinct feature of the fungus *Bipolaris maydis*. Similar types of conidial morphology and culture were previously observed from the isolates collected from various locations with different environmental conditions in India (Pal *et al.* 2015, Iddumu *et al.* 2021).

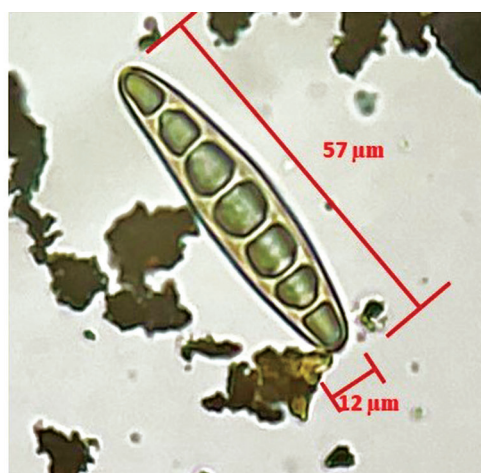
The molecular identification of the fungus resulted 509 bp for ITS, which showed 99.41% identity with *Bipolaris maydis* with 100% query coverage. The unique GenBank accession number was assigned to *Bipolaris maydis* as PP824365 by NCBI. Phylogenetic tree showed the close relation by forming one cluster with *Bipolaris maydis* isolate NDLS 1101 and *Bipolaris maydis* isolate BM21 having accession no. KX834885 (Fig. 2). In Indian scenario, ITS based molecular characterization and identification of *Bipolaris maydis* was previously carried out by Gogoi *et al.* (2014).

In planta efficacy of endophytic bacteria against MLB: Disease scoring was done two times at 20 and 30 DAI for both the *kharif* seasons. Among all the treatments, *Stentrophomonas maltophilia* at concentration 1.0 (T_3) performed the best with least PDI of 21.10% and 20.48% in the first and second season, respectively. Other treatments such as *Stentrophomonas maltophilia*, concentration 0.1

(T_2), *Brevundimonas olei*, concentration 1.0 (T_6) and *Pseudomonas aeruginosa* conc. 1.0 (T_9) rendered significantly less PDI as compared to negative control in both the seasons ($P \leq 0.05$). Nevertheless, *Stentrophomonas maltophilia* at concentration 1.0 (T_1) and *Brevundimonas olei*, concentration 1.0 (T_6) were statistically at par during the first season ($P \geq 0.05$). The pooled data of both the seasons recorded the least PDI of 20.79% with a minimum disease scoring



10 days old culture of *Bipolaris maydis* in OMA



Charateristic conidia of *Bipolaris maydis* with pseudosept at 400X

Fig. 1 Morpho-cultural characters of *Bipolaris maydis*.

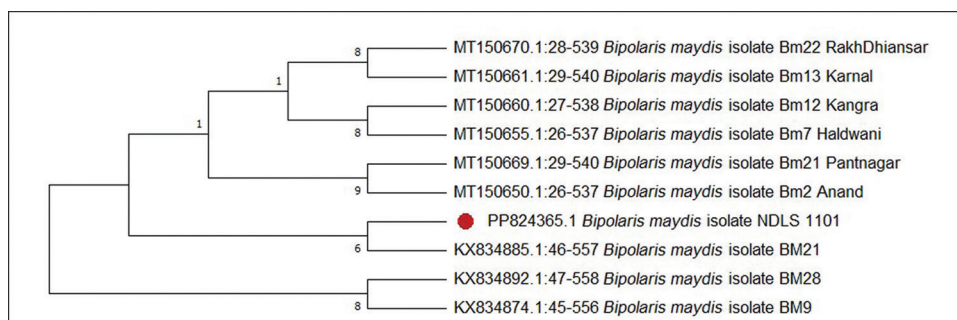


Fig. 2 Phylogenetic tree constructed using ITS sequences illustrates the relationship between the *Bipolaris maydis* isolate NDLS 1101 (Tagged with red colour circle) and other sequences available in the NCBI GenBank database.

of 1.93 proving the best performance among all other treatments (Table 1). Seed priming with *Stentrophomonas maltophilia* at a concentration of 0.1 (T_2) and *Pseudomonas aeruginosa* at 1.0 (T_9) showed satisfactory results with PDI 24.94% and 25.56%, respectively. PDI was observed to increase slightly in all the seed primed treatments when the concentration of bacteria was decreased. The efficacy of seed primed treatments were markedly superior, showed significantly better performance compared to fungicidal control with mancozeb 75% WP @2000 mg/L. There is limited research on this topic performed on maize crop, but various studies conducted on other crops have revealed the potential nature of endophytic bacteria against maize *Gibberella* ear rot (Mousa *et al.* 2015), rice blast (Kumar *et al.* 2021), ginger soft rot (Dinesh *et al.* 2015), early blight of tomato (Shoaib *et al.* 2019), and root rot of groundnut (Ma *et al.* 2023). The present study showed the promising biocontrol effects of *Stentrophomonas maltophilia* against MLB disease which also confirmed by Fariman *et al.* (2022)

antimicrobial activity.

Analysis of biochemical constituents of maize

Total sugars: Total sugar was estimated to know the infection mechanism of pathogen in host plant. The total sugar content was the highest in the pathogen inoculated treatments *Stentrophomonas maltophilia* at concentration 1.0 (T_3) followed by *Stentrophomonas maltophilia* at a concentration of 0.1 (T_2) and *Pseudomonas aeruginosa* at 1.0 (T_9). The lowest sugar accumulation was observed in negative control (T_{10}) after pathogen inoculation. The sugar content in absolute control (T_{12}) [pre and post MLB inoculation] remained similar with a slight change. In all the treatments, the total sugar content increased at post MLB inoculation (Fig. 3).

Earlier studies showed that the increase in sugar content in the host plant even after pathogen inoculation, which helps in maintaining plant vigour and also to increase resistance against pathogen (Dong and Beckles 2019). Elevated level of sugar content was also recorded in resistant lines of

Table 1 *In planta* evaluation of the efficacy of *Stentrophomonas maltophilia*, *Brevundimonas olei* and *Pseudomonas aeruginosa* against maydis leaf blight

Treatment	1 st season (2022)		2 nd season (2023)		Pooled	
	Score*	PDI (%) *	Score*	PDI (%) *	Score*	PDI (%) *
T_1 , SM (0.01)	2.47 ^h	26.78 ^g	2.30 ⁱ	26.03 ^{ef}	2.38 ^e	26.40 ^{ef}
T_2 , SM (0.1)	2.01 ^j	25.25 ^h	1.99 ^j	24.63 ^g	2.00 ^f	24.94 ^f
T_3 , SM (1.0)	2.00 ^j	21.11 ⁱ	1.85 ^k	20.48 ^h	1.93 ^f	20.79 ^g
T_4 , BO (0.01)	2.71 ^c	30.87 ^e	2.66 ^f	30.02 ^d	2.68 ^{cd}	30.44 ^c
T_5 , BO (0.1)	2.47 ^{gh}	28.33 ^f	2.36 ^g	27.34 ^e	2.42 ^d	27.84 ^d
T_6 , BO (1.0)	2.49 ^f	26.77 ^g	2.28 ^{hi}	25.38 ^{fg}	2.38 ^e	26.08 ^e
T_7 , PA (0.01)	3.02 ^c	34.57 ^c	3.08 ^d	33.10 ^c	3.05 ^b	33.84 ^b
T_8 , PA (0.1)	2.80 ^d	32.28 ^d	2.89 ^e	31.34 ^d	2.85 ^c	31.81 ^{bc}
T_9 , PA (1.0)	2.33 ⁱ	26.03 ^{gh}	2.11 ^j	25.10 ^{fg}	2.22 ^g	25.56 ^f
T_{10} , Negative control	5.87 ^a	70.00 ^a	5.04 ^a	71.26 ^a	5.45 ^a	70.63 ^a
T_{11} , Mancozeb	3.25 ^b	36.23 ^b	3.01 ^b	34.45 ^b	3.13 ^b	35.34 ^b
T_{12} , Absolute control	0.08 ^k	1.13 ^j	0.19 ^c	1.00 ⁱ	0.14 ^h	1.06 ^h

*Data are the mean of three replications. Significant differences between treatments are indicated by different letters in each column (Duncan multiple range test, $P \leq 0.05$). Disease data scored twice at 20 and 30 days interval.

SM, *Stentrophomonas maltophilia*; BO, *Brevundimonas olei* and PA, *Pseudomonas aeruginosa*.

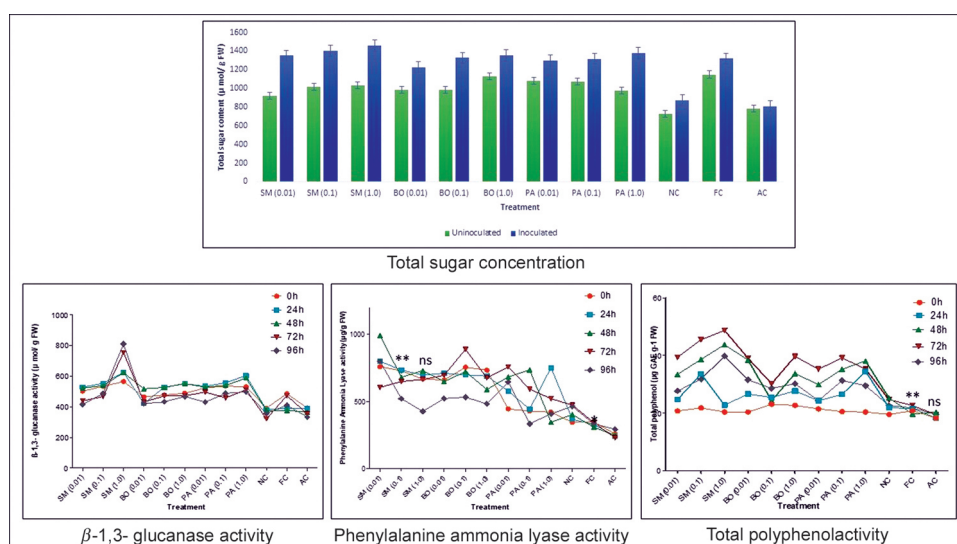


Fig. 3 Analysis of biochemical constituents, enzymatic antioxidant and non-enzymatic antioxidant activity in seed bacterized maize plant (CM 119) inoculated with *Bipolaris maydis*.

Activity was recorded at different time intervals starting from 0 h to 96 h after inoculation. A significant difference in enzyme activity is observed by Duncan's multiple range test (* where $P \leq 0.05$), (** where $P \leq 0.01$), and non-significant (ns where $P \leq 0.05$).

Treatment details are given under Materials and Methods.

maize during post MLB infection (Meshram *et al.* 2020). It was also observed that the sugar content in host plant was upregulated due to abiotic stress conditions (Thalmann and Santelia 2017).

Analysis of enzymatic antioxidant of maize

β -1,3- glucanase: The PR protein β -1,3- glucanase did not follow a definite trend over time; however, it showed a significant increase of its activity in the treatment *Stentrophomonas maltophilia* at 1.0 (T_3) at 72 h and 96 h as compared to the control ($P \leq 0.001$) (Fig. 3). In case of negative control (T_{10}), the enzyme activity was decreasing over time while in case of fungicidal control, the enzyme activity was increasing over time. There was no significant change observed in absolute control (T_{12}). Our findings on the activation of β -1,3- glucanase after *Bipolaris maydis* infection in endophytic treated maize supports earlier research on host plant defence mechanisms (Meshram *et al.* 2020). Similarly, another study conducted by Tian *et al.* (2007) suggested the enhanced activity of β -1,3- glucanase, induced by a biocontrol agent, could serve as a potential biochemical marker for defence against fungal pathogens in jujube. Recent studies on *Picea asperata* and other plants suggest that the increased activity of β -1,3-glucanase, triggered by biocontrol agents not only participates in pathogen defence but also improved plant resistance to multiple stresses (Liu *et al.* 2022).

Phenylalanine ammonia lyase: The activity of phenylalanine ammonia lyase (PAL) was significantly increased by the treatment *Stentrophomonas maltophilia* at concentration 0.01 (T_1) and *Brevundimonas olei* at concentration 0.1 (T_5) at 48 h and 72 h, respectively. The rest of other treatments recorded a similar pattern as compared

to the controls. The enzymatic activity was not significant in the case of *Stentrophomonas maltophilia* at conc. 1.0 (T_3) at 0 h and 72 h ($P \geq 0.05$) (Fig. 3). PAL activity was observed to be very low in the case of absolute control (T_{12}), followed by fungicidal control (T_{11}), negative control (T_{10}). In all the treatments, the PAL activity increased up to 72 h, considering *Brevundimonas olei*, concentration 0.1 (T_5) as an exception. In earlier studies on potential endophytes treated rice and tomato plants, the increase of PAL enzyme was reported up to 4th day or 72 h after challenge inoculation with *Rhizoctonia solani* (Kukreti *et al.* 2024) and *Alternaria solani* (Awan *et al.* 2018)

which then declined gradually. The timing of enhanced enzymatic expression patterns is highly crucial by balancing ROS which reduces the impact of pathogen invasion by detoxifying harmful chemicals (Khan *et al.* 2018). Another study showed *Stentrophomonas maltophilia* with enhanced PAL activity in potato, is recognized for its biocontrol capabilities, aiding in plant defence by increasing PAL enzyme activity, involved in the plant's resistance to *Ralstonia solanacearum* (Messiha *et al.* 2007).

Analysis of non-enzymatic antioxidant of maize

Total polyphenol: The total polyphenol activity in terms of μ g GAE/g FW was observed increasing up to 72 h and then decreasing substantially ($P \leq 0.001$). The highest polyphenol activity was recorded with *Stentrophomonas maltophilia* at concentration 1.0 (T_3) at 72 h and later declined drastically. The activity of polyphenol was statistically at par at 0 h and 24 h in absolute control (T_{12}) ($P \geq 0.05$). Similar to PAL, the activity of polyphenol was following a definite trend at different time points (Fig. 3). Recent studies indicated that *Stentrophomonas maltophilia* is known for its ability to activate defence enzymes involved in polyphenol biosynthesis, which increases as part of the potato plant's response to biotic stress, such as *Ralstonia solanacearum* (Messiha *et al.* 2007). Similarly, in *Arachis hypogea*, inoculation with *Stentrophomonas maltophilia* BJ01 increased total phenolic content (TPC), enhancing antioxidant activities and offering protection against abiotic stress, thereby promoting plant health and defence through polyphenol modulation (Alexander *et al.* 2019).

In conclusion, this study has demonstrated the potential effect of endophytic bacteria as an alternative to harmful fungicides to manage MLB disease in maize. The disease

resistance in maize as a result of interaction of maize genes at cellular as well as biochemical levels was evidenced. The results have provided the valuable insights of the promising effect of *Stenotrophomonas maltophilia* and *Brevundimonas olei* at concentrations 1.0 and 0.1, where the constitutional and induced biochemical compounds were recorded higher as compared to the control sets after pathogen inoculation. This not only shows effective disease control strategy by minimizing fungicidal application but also supports fostering a safer and more sustainable agricultural ecosystem. However, approval from relevant regulatory agencies would be required for the use of *Stenotrophomonas maltophilia* and *Brevundimonas olei* in biological control, as some strains of this bacteria have been linked to infections in immunocompromised individuals (Berg *et al.* 2005, Messiha *et al.* 2007). This study opens up the new path for molecular level study adopting whole transcriptomics analysis at different stages of crop growth to understand about the genetic level of defence activation in maize.

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