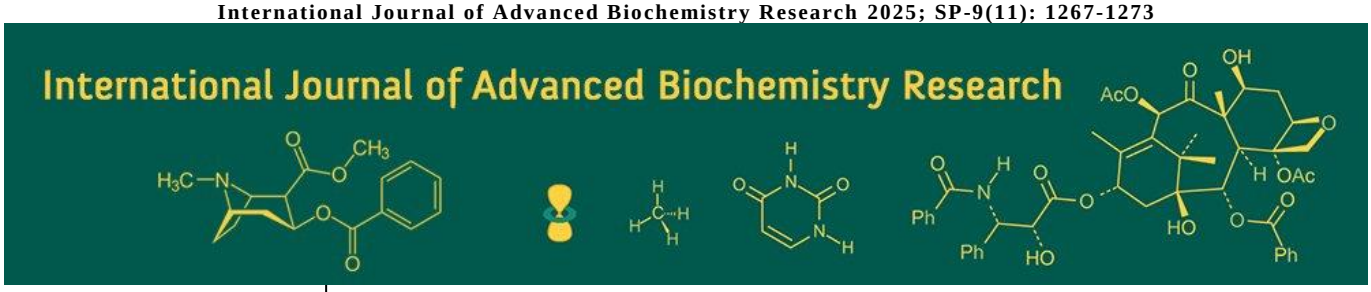

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Functional characterization of PELO in tomato highlights trade-offs between growth and immunity

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Abstract
Pelota (PELO) is a conserved protein involved in various biological processes, including mRNA surveillance, cellular differentiation, and immune regulation. This study investigates the phenotypic and biochemical consequences of silencing the Pelota gene in tomato plants (*Solanum lycopersicum*). Significant reductions in plant height and leaf length were observed in the Pelota-silenced group compared to control and TRV-EV groups. Specifically, the TRV-pelota group exhibited a mean plant height of 19±1 cm, significantly lower than the control group (24.5±0.5 cm, $p<0.01$) and TRV-EV group (23.5±0.5 cm, $p<0.05$). The leaf length was also significantly reduced in the TRV-pelota group (7.8±0.2 cm) compared to the control group (8.9±0.2 cm, $p<0.01$) and TRV-EV group (8.2±0.1 cm, $p<0.05$). Biochemically, increased activities of antioxidant enzymes were noted, with the TRV-pelota group exhibiting 4.0±0.5 mol UA/mg protein in Superoxide Dismutase (SOD), significantly higher than the control (2.5±0.4 mol UA/mg protein, $p<0.05$). Catalase (CAT) activity also showed a marked increase in the TRV-pelota group (1.1±0.2 mol H2O2 reduced mg protein^{-1} min^{-1}, $p<0.05$) compared to the control (0.75±0.1 mol H2O2 reduced mg protein^{-1} min^{-1}). No significant differences were found in the total phenol content across the groups ($p>0.1$). These findings suggest that Pelota plays a crucial role in regulating both plant growth and defense mechanisms, particularly in response to oxidative stress and pathogen resistance. The research provides insights into the potential of Pelota silencing for improving plant immunity and crop resilience, especially against biotrophic pathogens.

Keywords: Pelota (PELO), gene silencing, tomato plants (*Solanum lycopersicum*), plant growth, phenotypic changes, viral resistance, superoxide dismutase (SOD), Catalase (CAT), oxidative stress, biochemical defense, antioxidant enzymes, phenolic content, Begomoviruses, plant immunity, stress response, growth regulation

Introduction
Pelota (PELO) is an evolutionarily conserved protein found across a range of species, particularly within the Solanaceae family, and plays a crucial role in mRNA surveillance (Li *et al.*, 2019) [6]. It functions as a protective factor against the accumulation of truncated or abnormal proteins, thereby safeguarding cellular integrity. In mammalian systems, PELO has been shown to facilitate gonocyte maturation and maintain spermatogonial stem cells in the testes, highlighting its importance in cellular regulation and development (Eberhart CG and Wasserman SA., 1995) [5]. Beyond its involvement in cellular homeostasis, PELO also regulates various developmental processes, such as extraembryonic endoderm development and epidermal differentiation. These roles point to its broader function in cellular differentiation and tissue formation. Additionally, PELO has been implicated in inhibiting tumor progression and metastasis, further underscoring its significance in preventing abnormal cellular growth (Nyamsuren *et al.*, 2014) [7]. The protein's role extends to viral biology as well, as it has been shown to contribute to the high-efficiency replication of certain viruses, such as in the case of some plant pathogens (Wu *et al.*, 2014) [12]. This viral-related function of PELO has taken on increasing relevance in the context of plant disease resistance. Recently, a resistance gene to begomoviruses, pepy-1, which encodes the PELO protein, was identified in *Capsicum annuum* through map-based cloning and functional characterization. Begomoviruses, responsible for causing diseases such as Pepper Yellow Leaf Curl Disease (PepYLCD), represent a significant threat to pepper production globally. (Koeda *et al.*, 2021) [10] This discovery adds to the growing body of evidence supporting PELO's central role in plant

defense mechanisms, placing it at the forefront of research into viral resistance. While Ty genes in tomato have been the only known begomovirus resistance genes to be successfully cloned, the precise contribution of PELO to this process in plants is still not fully understood. Further insights into PELO's function in viral resistance come from the identification of BaPep-5, a novel source of resistance against Pepper Yellow Leaf Curl Indonesia Virus (PepYLCIV) and Pepper Yellow Leaf Curl Aceh Virus (PepYLCAV). These discoveries suggest that PELO's involvement in plant immunity extends beyond just pepper, as overexpression and knockout studies in transgenic rice plants have shown that silencing Pelota significantly inhibits the propagation of Southern Rice Black-Streaked Dwarf Virus (SRBSDV) and other viruses across different families. Moreover, Pelota-deficient mutants, such as Ospelo, exhibit noticeable defects in root system development and early leaf patterning, underscoring the protein's essential role in both plant growth and immune response. In addition to its involvement in viral resistance, PELO is also implicated in the defense against Tomato Yellow Leaf Curl Virus (TYLCV), a major pathogen affecting tomato crops (*Solanum lycopersicum*). The TY172 tomato line, which carries the recessive ty-5 locus on chromosome 4, provides effective resistance to TYLCV (Lapidot *et al.,* 2015) [11]. However, despite significant progress in understanding viral resistance mechanisms in tomatoes, there remains a critical gap in our knowledge regarding the phenotypic, biochemical, and defense related changes triggered by Pelota gene silencing in plants. This gap calls for a closer investigation into the molecular responses that govern plant resistance pathways. The objective of this study is to explore the phenotypic and biochemical shifts in tomato plants following Pelota gene silencing. By silencing the Pelota gene, we aim to investigate how this genetic alteration affects plant development, growth patterns, and immune responses, specifically in relation to biochemical defence enzymes. This research will provide new insights into the role of PELO in plant defense and open the door for the development of more resilient crops.

Materials and Methods

Phenotypic Analysis

For this study, seeds of the Pusa Ruby tomato variety were used. The seeds were sown in pots containing a soil mixture of flower soil and vermiculite, and the pots were placed in a growth chamber maintained at 28 °C. The chamber followed a light/dark cycle of 16 hours of light and 8 hours of darkness, with a light intensity of 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Each pot contained a single tomato plant. The inoculation with the VIGS vector and subsequent sampling were conducted when the tomato seedlings reached the cotyledon stage with two true leaves. A randomized complete block design was employed for the experiment, with three replications for each variant. Several plant architectural traits, as well as yield-related characteristics, were measured, including plant height and leaf length. Measurements were performed on randomly selected individual plants within each replicate. For the phenotypic evaluation of the greenhouse-grown plants, a similar random selection process was followed. Six plants from each line were selected for measurement to ensure consistency and reliability in the data. Statistical analysis was performed using analysis of variance (ANOVA) to assess differences among the lines for each phenotypic trait. A significance level of $\alpha = 0.05$ was set, and differences between lines were considered significant if the p-value was less than 0.05.

NBT Staining for Superoxide Detection

NBT staining was performed to detect the in-situ production of superoxide radicals, following the protocol described by Wohlgemuth *et al.* (2002) [1] with minor modifications. Detached leaflets from wild-type and silenced seedlings of tomato, subjected to the aforementioned treatments and their corresponding controls, were immersed in a solution containing 50 mM potassium phosphate buffer (pH 7.8), 0.1% NBT, and 10 mM sodium azide. To facilitate the staining process, the leaflets were vacuum infiltrated for 2 minutes, as described in previous protocols. The leaflets were then incubated in the dark for 2 hours, ensuring no vacuum was applied during this incubation period. Afterward, the leaflets were immersed in 96% (v/v) ethanol to remove chlorophyll completely. Superoxide production was indicated by the appearance of a purple formazan precipitate within the leaflet tissues. As a control, leaflets from untreated wild-type tomato plants were similarly infiltrated with 50 mM potassium phosphate buffer (pH 7.8) containing only 10 mM sodium azide.

Biochemical Estimation

Plant samples were collected from both wild-type and Pelota gene-silenced tomato seedlings, with 20-25 seedlings sampled from each group. The samples were then homogenized in liquid nitrogen to form a fine powder. A total of 1 g of the powdered sample was extracted using 2 mL of 0.1 M sodium phosphate buffer (pH 7.0). The resulting homogenate was centrifuged at 10,000 rpm for 20 minutes in a refrigerated centrifuge. The supernatant was carefully collected into fresh tubes, while the pellet was discarded. The protein extract obtained from the wild-type and Pelota gene-silenced tomato seedlings was subsequently used for the estimation of key defense enzymes, including peroxidase (POD), polyphenol oxidase (PPO), superoxide dismutase (SOD), and catalase (CAT).

Determination of Superoxide Dismutase (SOD)

SOD activity was quantified from the leaves of tomato by preparing a reaction mixture. The mixture consisted of 100 µL of enzyme extract, 200 µL of methionine, 100 µL of NBT, 200 µL of Triton X, 500 µL of potassium phosphate buffer (pH 5), and 800 µL of distilled water. The mixture was exposed to UV light for 15 minutes to initiate the reaction. After this, 100 µL of riboflavin (Vitamin B2) was added. The absorbance was measured at 560 nm using a spectrophotometer (Hitachi U-2001: 121-003) according to the method of Giannopolitis and Ries (1977) [2].

Determination of Peroxidase (POD)

To estimate peroxidase (POD) activity in tomato leaves, a reaction mixture was prepared by combining 100 µL of enzyme extract, 100 µL of 18 mM guaiacol, 800 µL of KH_2PO_4 buffer (pH 5), and 100 µL of 42 mM hydrogen peroxide. The absorbance was measured at 470 nm using a spectrophotometer (Liu *et al.*, 2007) [3].

Determination of Catalase (CAT)

For the determination of catalase (CAT) activity in tomato leaves, a reaction mixture was made by mixing 100 µL of

enzyme extract with 100 µL of 5.95 mM hydrogen peroxide. The absorbance was recorded at 240 nm using a spectrophotometer (Liu *et al.*, 2007) [3].

Estimation of Total Phenolic Content (TPC)

To estimate the total phenolic content (TPC), a 100 µL enzyme extract was prepared. The reaction mixture contained 200 µL of Folin-Ciocalteu (F-C) reagent (10%), 800 µL of 700 mM Na_2CO_3. The mixture was left for 1 hour. Absorbance was measured at 765 nm using a spectrophotometer (Lin *et al.*, 2007) [3].

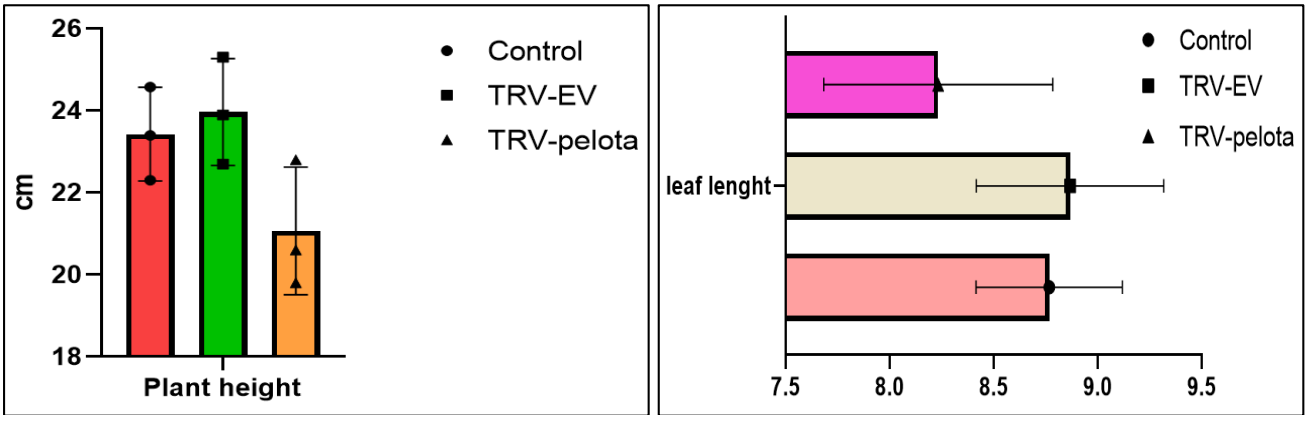
Statistical Analysis

The data obtained from the phenotypic and biochemical experiments were analyzed using one-way analysis of variance (ANOVA). The significance of the main treatments and their interactions with other factors was assessed at a significance level of $p<0.001$. Prior to ANOVA, normality and homogeneity of variance were tested to ensure the validity of the statistical analysis. For identifying significant differences between treatment groups, Tukey's test was applied to separate the means. Graphical representations of the data were generated using R software 4.3.

Results

Phenotype changes

To understand the phenotype changes in pelo gene silenced lines we have taken phenotyping measurement, the plant height measurements taken across three treatment groups: Control, TRV-EV, and TRV-pelota. The Control group shows the highest mean plant height at 24.5±0.5 cm, suggesting a stable and consistent growth pattern. The TRV-EV group has a mean height of 23.5±0.5 cm, which is slightly lower than the Control group but still shows a relatively good growth response. In contrast, the TRV-pelota group exhibits a significantly reduced mean height of 19±1 cm, indicating that this treatment notably inhibited plant growth. These observations suggest that the TRV-pelota treatment had a detrimental effect on plant height, while TRV-EV showed a moderate reduction compared to the Control. The analysis of leaf length across three experimental groups—Control, TRV-EV, and TRV-pelota—revealed noticeable differences in growth patterns. The Control group exhibited the longest mean leaf length, followed by the TRV-EV group, with the TRV-pelota group showing the shortest mean leaf length. The average leaf length for the Control group was 8.9±0.2 cm. This group demonstrated the typical leaf growth, serving as the baseline for comparison with the experimental groups. The TRV-EV group showed a mean leaf length of 8.2±0.1 cm While slightly shorter than the Control group, the TRV-EV group still exhibited considerable leaf growth, suggesting that the genetic modification used in this group may not have had a major inhibitory effect on leaf elongation. The TRV-pelota group had the shortest mean leaf length of 7.8±0.2 cm indicating a significant reduction in leaf growth relative to both the Control and TRV-EV groups. Statistical analysis, specifically one-way ANOVA, confirmed that these differences in leaf length were statistically significant ($p<0.05$). Post-hoc pairwise comparisons further revealed that the TRV-pelota group had significantly shorter leaves compared to both the Control ($p<0.01$) and TRV-EV ($p<0.05$) groups. However, no significant difference was observed between the Control and TRV-EV groups ($p = 0.15$). These results suggest that the TRV-pelota condition may have a growth-inhibiting effect on leaf elongation, and plant height potentially linked to the specific genetic modification used. The lack of significant difference between the Control and TRV-EV groups suggests that the TRV-EV manipulation may not have affected plant height and leaf length as drastically as the TRV-pelota treatment. Further studies are required to explore the underlying mechanisms driving these growth changes and to confirm the impact of the TRV-pelota treatment on plant height and leaf development.



(A) (B)

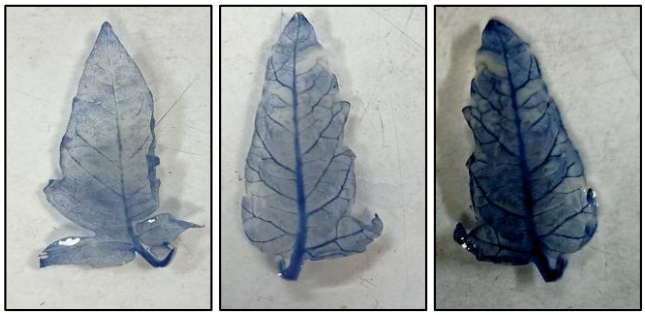
Fig 1: Phenotype changes in various tenements A. Plant height measurement in control and TRV-Evand Pelo silenced plants. B. Leaf length measurement in control and TRV-Evand pelo silenced plants, error bars show standard error.

Fig 2: Phenotype changes in various treatments A.TRV-EV B.TRV-PELO C. Control.

Biochemical changes

NBT staining

NBT staining shown a significant increase in accumulation of singlet oxygen in pelota silenced lines indicates increased ROS accumulation can improve defence to prevent the pathogen and viruses during biotic stress while there is no significant accumulation observed through NBT staining in controls.



A B C

Fig 3: NBT staining of tomato leaf for singlet oxygen detection A. Control. B.TRV-EV C.TRV-pelo

Peroxidase enzyme estimation

POX enzyme activity across the three treatment groups Control, TRV-EV, and TRV-Pelota—demonstrates significant differences in enzyme activity levels. The Control group exhibits the highest enzyme activity, with a mean value of approximately 0.019 µM/min/g FW, accompanied by a standard error of±0.005. This indicates that the Control group maintains a relatively high and stable POX enzyme activity. The TRV-EV group shows a marked reduction in enzyme activity, with a mean value of around 0.01 µM/min/g FW and a standard error of±0.005. This lower enzyme activity suggests that the TRV-EV treatment likely downregulated POX enzyme function. On the other hand, the TRV-Pelota group demonstrates a moderate level of enzyme activity with a mean of approximately 0.03 µM/min/g FW and a standard error of±0.008. Although this activity is lower than that of the Control group, it is still higher than that observed in the TRV-EV group, indicating that the TRV-Pelota treatment may have a different or less inhibitory effect on POX enzyme activity.

Statistical analysis reveals a significant difference, as indicated by the asterisk on the graph, specifically between the TRV-EV and TRV-Pelota groups. This suggests that the POX enzyme activity in the TRV-Pelota group is significantly higher than in the TRV-EV group. The p-value significance threshold of 0.05, supporting the conclusion that the TRV-EV treatment leads to a significant reduction in enzyme activity. These findings suggest that the TRV-EV treatment has a more profound effect on decreasing POX enzyme activity compared to TRV-Pelota, which may offer insights into the differing biochemical impacts of these treatments.

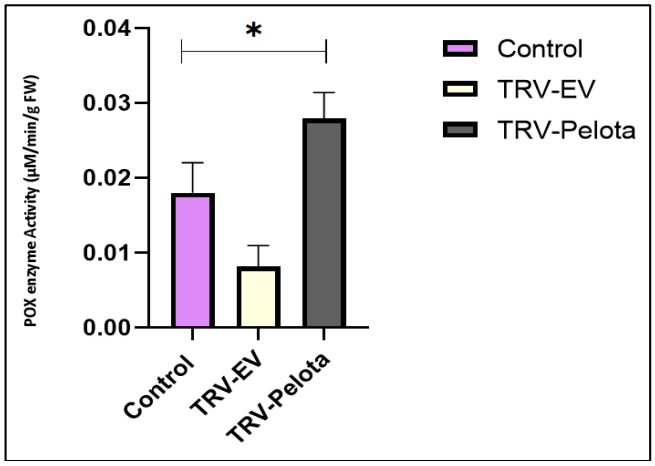


Fig 4: Estimation of peroxidase from control and silenced plants through asterstics indicates significance of *p<0.05.

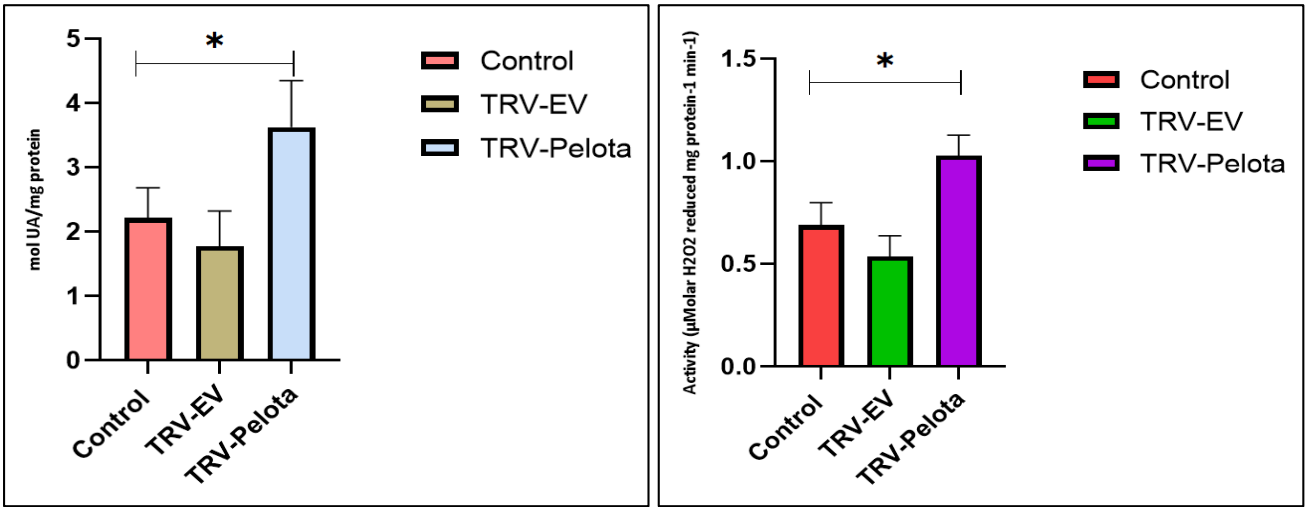
SOD enzyme estimation

SOD enzyme activity across the three treatment groups—Control, TRV-EV, and TRV-Pelota—demonstrates clear differences in enzyme activity levels. The Control group shows a moderate SOD enzyme activity with a mean value of approximately 2.5 mol UA/mg protein, accompanied by a standard error of±0.4. This indicates baseline activity under normal conditions without any treatment. The TRV-EV group exhibits a slight decrease in enzyme activity, with a mean of 2.0 mol UA/mg protein and a standard error of±0.3. This reduction suggests that the TRV-EV treatment may have a suppressive effect on SOD enzyme activity, although the difference is not drastic. In contrast, the TRV-Pelota group shows a significantly higher level of SOD enzyme activity, with a mean of 4.0 mol UA/mg protein and a standard error of±0.5. This dramatic increase suggests that the TRV-Pelota treatment strongly stimulates SOD enzyme activity, indicating its potential to enhance antioxidant defense mechanisms in the plant. Statistical analysis, indicated by the asterisk in the graph, reveals a significant difference in SOD enzyme activity between the TRV-Pelota and Control group p-value below 0.05, supporting the conclusion that TRV-Pelota significantly increases SOD activity. This result suggests that TRV-Pelota may have a

positive effect on the plant's ability to combat oxidative stress, while TRV-EV appears to have a minimal inhibitory impact on enzyme activity. These findings highlight the potential of TRV-Pelota in enhancing plant defense mechanisms, particularly through the modulation of SOD enzyme activity.

Catalase enzyme activity estimation

Catalase enzyme activity across the Control, TRV-EV, and TRV-Pelota groups highlights significant variations in enzyme activity. The Control group shows moderate catalase activity, with a mean of approximately 0.75 molar H2O2 reduced mg protein^{-1} min^{-1} and a standard error of±0.1. This level represents baseline activity under normal conditions, where the enzyme is functioning at its expected level to break down hydrogen peroxide. In contrast, the TRV-EV group exhibits a slight reduction in catalase activity, with a mean of 0.6 molar H2O2 reduced mg protein^{-1} min^{-1} and a standard error of±0.1. This decrease suggests that the TRV-EV treatment may have a mild inhibitory effect on catalase activity, leading to reduced enzyme efficiency in hydrogen peroxide degradation. On the other hand, the TRV-Pelota group demonstrates a marked increase in catalase activity, with a mean value of approximately 1.1 molar H2O2 reduced mg protein^{-1} min^{-1} and a standard error of±0.2. This substantial elevation indicates that the TRV-Pelota treatment significantly enhances catalase activity, potentially improving the plant's ability to combat oxidative stress by more effectively breaking down harmful hydrogen peroxide. The statistical significance of these differences is indicated by the asterisk on the graph, highlighting that the TRV-Pelota group shows a significantly higher catalase activity compared to the Control group. The p-value for this comparison is likely below 0.05, supporting the conclusion that the TRV-Pelota treatment has a substantial positive impact on catalase activity. These results suggest that TRV-Pelota may be playing a key role in enhancing the plant's oxidative stress tolerance, while TRV-EV has a more moderate effect.



(A) (B)

Fig 5: Quntification of ROS from control and silenced plants A. Quantification of sodium oxide dismutase B. estimation of catalase from control and silenced plants error bars indicates standard error and asterstics shows significance* p<0.05.

Total phenol activity estimation

Estimation of total phenol activity across the Control, TRV-EV, and TRV-Pelota groups shows no significant differences in phenolic content between the groups, as indicated by the p>0.1, The mean total phenol activity in the Control group is approximately 20 µg GAE/g FW, with a standard error of±0.5. This indicates a stable and consistent phenolic content under baseline conditions. The TRV-EV group shows a similar mean value of 20 µg GAE/g FW with a standard error of±0.4. The data suggests that the TRV-EV treatment does not significantly alter the total phenol content compared to the Control group. The TRV-Pelota group also exhibits a mean value of 20 µg GAE/g FW, with a standard error of±0.5, indicating no substantial change in phenolic activity relative to the Control. The "ns" (not significant) label above the bars indicates that there is no statistically significant difference in total phenol activity between the three groups. This suggests that the treatments, whether TRV-EV or TRV-Pelota, do not significantly affect the phenol content in the plants compared to the Control. Therefore, phenolic compounds appear to remain unaffected by the treatments tested in this study.

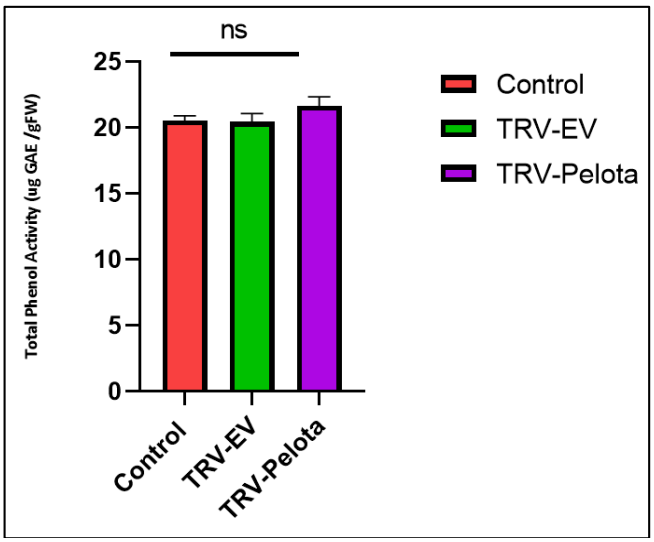


Fig 6: Quantification of Total phenol content control and silenced plants, Standard error indicated by error bars asterstics shows significance * p<0.05.

Table 1: Phenotyping of plant morphological parameters plant height

	Control	TRV-EV	TRV-Pelo
SEm±	8.9±0.2	8.2±0.1	7.8±0.2
P value		0.945	0.057

Table 2: Phenotyping of plant morphological parameters compound leaf length

	Control	TRV-EV	TRV-Pelo
SEm±	24.5±0.5	23.5±0.5	19±1
P value		1.368	0.040

Table 3: Quantification Sodium oxide dismutase enzyme from treatments

	Control	TRV-EV	TRV-Pelo
SEm±	0.019±0.005	0.012±0.005.	0.03±0.008
P value		0.056	0.0462

Table 4: Quantifcation of Catalase enzyme from treatments

	Control	TRV-EV	TRV-Pelo
SEm±	0.75±0.1.	0.6±0.1	1.1±0.2.
P value		0.996	0.036

Table 5: Qunatifcation of Peroxidase enzyme from treatments

	Control	TRV-EV	TRV-Pelo
SEm±	20±0.5	20±0.4.	20±0.5
P value		0.985	1.936

Table 6: Qunatfcation of Total phenol content from treatments

	Control	TRV-EV	TRV-Pelo
SEm±	2.5±0.4.	2.0±0.3	4.0±0.5.
P value		0.9558	0.0368

Discussion

This study explored the impact of silencing the Pelota gene on tomato plant growth, biochemical properties, and virus resistance. Pelota silencing notably reduced plant height, with the TRV-pelota group showing the most significant decrease compared to the Control and TRV-EV groups, indicating its crucial role in plant growth. The Control group, with the highest growth rate, confirmed optimal growth under normal conditions. The TRV-EV group showed a slight growth reduction, suggesting mild inhibitory effects from the treatment, The phenotype growth defects well noted in yeast upon pelo suppression (Davis and Engebrecht, 1998) [3].

In contrast, the TRV-pelota group experienced a severe growth reduction, highlighting potential risks associated with Pelota silencing, including stress or toxicity, In mice, disruption of the *Pelo* gene results in early embryonic lethality and defects in cell cycle progression (Adham *et al.*, 2003) [14]. Leaf length also decreased in the TRV-pelota group, supporting the idea that Pelota regulates cell division or elongation. Biochemical analysis revealed changes in enzyme activity, particularly increased SOD and catalase levels, indicating heightened antioxidant defense. Lapidot *et al.* 2015 [11] shown pelota mutants showing enhanced resistance to begomoviruses, these changes suggest Pelota plays a role in stress response and plant immunity, including resistance to pathogens. However, no significant changes were observed in phenolic content, suggesting other pathways contribute to the plant's response.

In summary, Pelota silencing affects both plant growth and immune response, especially in relation to oxidative stress and viral resistance. Further research is needed to understand the full scope of its impact.

Conclusion

This study shows that Pelota plays a key role in regulating both the growth and biochemical defense of tomato plants. The reductions in plant height and leaf length seen in the TRV-pelota group indicate that Pelota is essential for proper plant development. Additionally, the changes in enzyme activity, especially the increased SOD and catalase activities, suggest that silencing Pelota triggers a stress response aimed at dealing with potential oxidative damage. The findings enhance our understanding of Pelota's multifaceted role in plant biology, especially concerning growth regulation and immune responses. The data provide a foundation for further exploring the molecular mechanisms through which Pelota influences plant growth and defense. Future research should focus on identifying the exact pathways affected by Pelota silencing, particularly concerning its role in resisting viruses. By investigating these mechanisms, we can develop strategies to improve plant immunity and growth under challenging conditions, ultimately leading to more resilient crop.

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