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Biochemical Basis of Resistance in *Oryza rufipogon* (Wild rice) against *Meloidogyne graminicola* and *Drechslera oryzae* in Punjab

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Abstract: Rice (*Oryza sativa* L.), a staple food for over half of the global population, faces severe yield losses due to biotic stresses, notably the rice root knot nematode (*Meloidogyne graminicola*) and brown leaf spot pathogen (*Drechslera oryzae*). These pathogens significantly affect root function and overall plant health. This study investigates the biochemical basis of resistance in *Oryza rufipogon* (wild rice) accessions against these pathogens by analyzing key defense-related enzymes and compounds. Two resistant and two susceptible accessions of *O.rufipogon* were evaluated against *M. graminicola* alone, along with accessions resistant and susceptible to both pathogens. Biochemical parameters including PAL (phenylalanine ammonia lyase), TAL (tyrosine ammonia lyase), peroxidase, total phenols, ortho-dihydroxy phenols and total proteins were quantified post-inoculation. There were significantly higher activity of all enzymes and phenolic compounds in resistant accessions compared to susceptible ones under both single and combined pathogen inoculations. Increased activity of PAL and TAL suggests enhanced lignin biosynthesis, aiding structural defense. Elevated peroxidase activity indicates a stronger reactive oxygen species (ROS) detoxification response, while higher phenol levels point to the activation of redox-based defenses. The findings suggest that resistance in *O. rufipogon* is strongly associated with upregulation of specific biochemical pathways and can serve as a foundation for developing resistant rice cultivars. This study provides valuable insights into host-pathogen interactions and the role of biochemical markers in rice defense mechanisms.

Keywords: Biochemical resistance, *Oryza rufipogon*, wild rice, *Meloidogyne graminicola*, *Drechslera oryzae*

1. INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most significant staple crops globally, feeding over half of the world's population and serving as a crucial source of calories and livelihood (FAO, 2021). However, rice production is continually threatened by various biotic and abiotic stresses with pathogens posing a major constraint. Among these, *Meloidogyne graminicola* (rice root-knot nematode) and *Drechslera oryzae* (causal agent of brown leaf spot) are increasingly recognized for their detrimental effects on rice growth and yield. *M. graminicola* is a soil-borne endoparasitic nematode that causes the formation of giant cells in rice roots, disrupting the vascular system and ultimately reducing nutrient and water uptake (Mantelin et al., 2017). This nematode poses a significant threat to both nursery-raised and direct-seeded rice systems, especially in rainfed and lowland ecologies. Similarly, *D. oryzae*, the fungal pathogen responsible for brown leaf spot, is a seed- and soil-borne disease known to cause considerable yield losses in susceptible cultivars, particularly under nutrient-deficient conditions (Surendhar et al., 2022).

In plant-pathogen interactions, biochemical defense responses are activated upon infection. These responses include the induction of phenolic compounds, defensive enzymes and protein synthesis, all of which play essential roles in plant resistance mechanisms (Saha et al., 2016). Phenolic compounds-particularly total phenols and ortho-dihydroxy phenols-are involved in reactive oxygen species (ROS) scavenging, strengthening of cell walls via lignification and direct antimicrobial activity (Pant et al., 2014; Senthilkumar et al., 2007). The accumulation at the infection site can lead to hypersensitive response and restricted pathogen growth (Ranchana et al., 2015). Among the enzymes implicated in plant defense, phenylalanine ammonia-lyase (PAL) and tyrosine ammonia-lyase (TAL) serve as critical entry point enzymes into the phenylpropanoid pathway leading to the synthesis of lignin, flavonoids and other defense-related compounds (Barros et al., 2016). Similarly, peroxidases are involved in the detoxification of H_2O_2 and catalyze the polymerization of phenolic compounds into lignin, contributing to cell wall reinforcement and pathogen restriction (Falade et al., 2017).

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The activity of these enzymes has been observed to be significantly higher in resistant genotypes of various crops, including rice, brinjal, and tomato, upon nematode or fungal infection (Nayak and Pandey, 2016).

Understanding the biochemical basis of resistance to both *M. graminicola* and *D. oryzae* is critical for developing durable disease-resistant rice varieties. Despite the economic significance of these pathogens, limited information is available on the biochemical and enzymatic changes associated with resistance in wild rice accessions such as *Oryza rufipogon*, a known reservoir of resistance genes (Kalaiarasan, 2009). The present study was undertaken to explore the biochemical basis of resistance to *M. graminicola* and *D. oryzae* in selected resistant and susceptible accessions of *O. rufipogon*. Specifically, the study aimed to quantify the activity of defense-related enzymes (PAL, TAL, and peroxidase), phenolic compounds (total phenols and ortho-dihydroxy phenols) and total soluble proteins post-infection. These insights may contribute to the identification of potential biomarkers for resistance breeding in rice.

2. MATERIALS AND METHODS

In order to understand the basis of rice root knot nematode (*M. graminicola*) and brown leaf spot (*D. oryzae*) resistance, biochemical analysis of two resistant and two susceptible accessions of *O. rufipogon* against *M. graminicola* and combined inoculation of *M. graminicola* and *D. oryzae* was done in 2020-2021 in Department of Basic Sciences of Punjab Agricultural University, Ludhiana. The accessions were: IR93070 and CR100381 (Resistant to *M. graminicola*), IR104844 and IR105494 (Susceptible to *M. graminicola*), IR104821 and IR105375 (Resistant to both pathogens *i.e. M. graminicola* and *D. oryzae*) and CR100381 and CR100006A (Susceptible to both *M. graminicola* as well as *D. oryzae*). The biochemical parameters include enzymes (phenylalanine ammonia lyase (PAL), tyrosine ammonia lyase (TAL) and peroxidase), orthrohydroxy phenols, total phenols and total proteins. Biochemical assays were done on the roots of these genotypes. Sixty days following infection, the test plants were harvested. The soil was then carefully shaken away from the roots of the plants. The harvested rice roots were cleaned separately and dried with tissue paper before being examined for biochemical changes.

Extraction and assay of phenylalanine ammonia lyase (PAL) assay was performed as per method of Hadwiger and Schwochau (1971) while Tyrosine ammonia lyase (TAL) was done as per method given by Burrell and Rees (1974). Peroxidase extraction and assay was performed as method given by Shannon et al. (1966). The post-infectional changes in the level of ortho-dihydroxy phenols were studied using the colorimetric method of Nair and Vaidyanathan (1964). In addition to this, extraction of phenol and determination of total soluble proteins was also done.

2.1. Statistical Analysis

The differences among means were compared by Tukey method ($P<0.05$) using IBM SPSS software v.27.0.

3. RESULTS AND DISCUSSION

3.1. Biochemical Changes in Resistant and Susceptible Accessions of *O. rufipogon* after Inoculation of *M. graminicola*

3.1.1. Biochemical changes in enzymes: The data on effect of *M. graminicola* infestation on enzymes in roots of *O. rufipogon* depicts that the activity of all enzymes was more in resistant accessions as compared to susceptible ones. The activity of PAL was higher in both the resistant accessions. The PAL values in accession IR93070 and CR100381 (resistant to *M. graminicola*) was 0.072 and 0.068 u mol of t-cinnamic acid min^{-1} g^{-1} of FW respectively whereas the activity of this enzyme in susceptible accessions *viz*., IR105494 and IR104844 was 0.029 and 0.040 u mol of t-cinnamic acid min^{-1} g^{-1} of FW respectively.

The activity of tyrosine ammonia lyase (TAL) was highest in the resistant accessions IR93070 and CR100381. TAL activity in these accessions was 0.053 and 0.061 μ mol of t-cinnamic acid min^{-1} g^{-1} fresh weight (FW) respectively. In contrast, susceptible accessions showed markedly lower TAL activity. The minimum TAL activity was recorded in IR105494 and IR104844, with values of 0.011 and 0.014 μmol of t-cinnamic acid min^{-1} g^{-1} FW, respectively. Similarly, peroxidase activity was significantly higher in *O. rufipogon* resistant accessions than in susceptible ones. Peroxidase activity in IR93070 and CR100381 was 5.17 and 4.24 OD min^{-1} g^{-1} FW, respectively, whereas much lower activity was observed in the susceptible accessions IR105494 and IR104844, with values of 0.69 and 0.62 OD min^{-1} g^{-1} FW, respectively (Table 1).

3.1.2. Biochemical changes in total phenols (ug/g), Orthrohydroxy phenols (ug/g) and total proteins (mg/g): The activity of total phenols was significantly affected when *M. graminicola* was inoculated on resistant and susceptible accessions of *O. rufipogon*. After nematode inoculations, the total phenol activity was expressed more in roots of both resistant accessions as compared to susceptible. Value of total phenols was observed to be 214.12 and 236.20 ug/g in IR93070 and CR100381 accessions (Resistant) while the values were 69.76 and 73.31 ug/g in IR105494 and IR104844 accessions (Susceptible accessions). Rice roots treated with *M. graminicola* expressed significantly higher amount of orthrohydroxy phenols in resistant accessions of *O. rufipogon*. The amount of orthrohydroxy phenols in resistant accessions *viz*., IR93070 and CR100381 was observed to be 15.31 and 16.25 ug/g while it was observed to be comparatively less in susceptible accessions *viz*., IR105494 (4.75 ug/g) and IR104844 (3.99 ug/g). The activity of total proteins was also observed to be higher in resistant accessions as compared to susceptible accessions (Table 1).

3.1.3. Biochemical changes in resistant and susceptible accessions of *O. rufipogon* after combined inoculation of *M. graminicola* and *D. oryzae*: The activity of enzymes TAL, PAL and peroxidase in combined inoculation of rice root knot nematode and brown leaf spot was found to be higher in resistant accessions (IR104821 and IR105375) while decreased in susceptible accessions (CR100381 and CR100006A). The PAL values were 0.073 and 0.084 u mol of t-cinnamic acid min^{-1} g^{-1} of FW in resistant accessions *i.e.* IR104821 and IR105375 while PAL values decreased to 0.009 and 0.013 u mol of t-cinnamic acid min^{-1} g^{-1} of FW in susceptible accessions *viz*., CR100381 and CR100006A. The TAL also showed the similar activity and was more in both the resistant accessions and lower in susceptible accessions. Similarly the activity of peroxidase was higher in resistant accessions and lower in susceptible accessions.

The combined inoculation of both the pathogens also affected the activity of orthrohydroxy, total phenols and total proteins in resistant and susceptible accessions. The activity of all these parameters was more in resistant accessions and decreased in susceptible ones when combined inoculation of both pathogens was done. The orthrohydroxy phenols was 18.43 and 20.60 ug/g in IR104821 and IR105375 accessions and 2.49 and 2.92 ug/g in CR100381 and CR100006A accessions. The total proteins were also more in resistant accessions IR104821 and IR105375 (30.57 and 33.18 mg/g) as compared to susceptible accessions CR100381 and CR100006A (7.28 and 8.30 mg/g). Similarly, in case of total phenols the activity was higher in resistant accessions as compared to susceptible. The activity of all enzymes, orhtohydroxy phenols, phenols and total proteins was decreased more in the treatments where combined inoculation of both pathogens (*M. graminicola* and *D. oryzae*) was done as compared to nematode alone (*M. graminicola*) in both resistant and susceptible accessions of *O. rufipogon* (Table 2).

Rice root knot nematode (*M. graminicola*) and brown leaf spot pathogen (*D. oryzae*) significantly affect root function and overall plant health. Plants undergo morphological and biochemical changes in response to these pathogens. There was significant increases in enzymes (PAL, TAL, and peroxidase activity), orthrohydroxy phenols, total proteins and phenols in resistant accessions and significant decrease in susceptible accessions. Phenolic compounds in plants play a vital role in their defence system, particularly redox response and free radical scavenging (Saha et al., 2016). Accumulation of phenols at the site of infection is characteristics in plant defence response and cause rapid cell death and prevents penetration of pathogens (Pant et al., 2014). The increase in phenolics in resistant plants is due to high activity of α-glycosidase, which converts non-toxic phenolic glycosides to toxic phenolic which are inhibitory to the pathogen. These phenolic compounds are possibly converted by increased peroxidase

Table 1. Biochemical changes in roots of susceptible and resistant *O. rufipogon* accessions after inoculation with *M. graminicola*

Pathogen	Accessions	Phenol (ug/g)	Total proteins (mg/g)	PAL (u mol of t-cinnamic acid min^{-1} g^{-1} of FW)	TAL (n mol of p-coumaric acid min^{-1} g^{-1} of FW)	Orthohydroxy phenols (ug/g)	Peroxidase (OD min^{-1} g^{-1} of FW)
Nematode only	Resistant var I-IR93070	214.12[ab]	30.27[a]	0.072[a]	0.053[ab]	15.31[b]	5.17[a]
	Resistant varII-CR100381	236.20[ab]	32.92[a]	0.068[a]	0.061[a]	16.25[b]	4.24[a]
Nematode only	Susceptible var I-IR105494	69.76[c]	11.55[b]	0.029[bc]	0.011[c]	4.75[c]	0.69[b]
	Susceptible varII-IR104844	73.31[c]	13.56[b]	0.040[b]	0.014[c]	3.99[c]	0.62[b]

Means sharing common letters within columns do not differ significantly by Tukey's test at P < 0.05%

Table 2. Comaparative analysis of biochemical parameters in susceptible and resistant *O. rufipogon* accessions inoculated with *M. graminicola* and *D. oryzae*

Pathogen	Accessions	Phenol (ug/g)	Total proteins (mg/g)	PAL (u mol of t-cinnamic acid min^{-1} g^{-1} of FW)	TAL (n mol of p-coumaric acid min^{-1} g^{-1} of FW)	Orthohydroxy phenols (ug/g)	Peroxidase (OD min^{-1} g^{-1} of FW)
Nematode+ Brown leaf spot	Resistant var I-IR104821	211.29[b]	30.57[a]	0.073[a]	0.058[ab]	18.43[ab]	5.12[a]
	Resistant var II-IR105375	241.19[a]	33.18[a]	0.084[a]	0.043[b]	20.60[a]	5.92[a]
Nematode+ Brown leaf spot	Susceptible var I-CR100381	55.38[c]	7.28[c]	0.009[d]	0.009[c]	2.49[c]	0.27[b]
	Susceptible var II-CR100006A	57.55[c]	8.30[c]	0.013[cd]	0.008[c]	2.92[c]	0.38[b]

Means sharing common letters within columns do not differ significantly by Tukey's test at P < 0.05%

activity to quinines in resistant cultivars and quinines are reported to be more toxic to microorganism. The quick breakdown of bound phenols and switching of phenols to alternative pathways leading to the creation of different compounds like lignin, which plays a crucial role in resistance, could explain the increase in phenolic compounds during infection (Senthilkumar et al., 2007).

Another mode of action of phenolic compounds may be related to the modification of the nematode physiology. RKNs secrete a pool of substances into the plant cell membrane to induce nematode feeding site formation (Williamson and Gleason, 2003, Cailaud et al., 2008). It has been proposed that such secretion may be induced by some phenolic compounds such as resorcinol, catechol, hydroquinone and caffeic acid (Jaubert et al., 2002). Ranchana et al. (2015) also concluded that the roots of nematode resistant tuberose genotype (Kahikuchi Single) retain highest phenolic content after inoculation indicating the use of resistant genotype as one of the parent to develop hybrids. Rani et al. (2008) also recorded that degree of resistance to root knot nematode is indicated by the increased phenolic content which may cause browning and resistant mechanism in the roots of tomato. Kalaiarasan (2009a) also observed higher total phenol content due to root knot nematode infestation. In addition to this, Bisen et al. (2015) also observed that higher amount of total phenol in rice leaves resulted lower disease incidence of *D. oryzae.*

Similarly, orthodihydroxy phenol content of different *O. rufipogon* accessions increased in the roots after inoculations. Nayak and Pandey (2016) observed enhanced peroxidase activity in nematode inoculated samples of both susceptible and resistant brinjal cultivars, although resistant cultivars had higher enzymatic activity. Ashfaq et al. (2021) also found that the brown leaf spot resistant phenotypes in rice line (PARC-7) reflect the higher accumulation of phenylalanine ammonia lyase, polyphenol oxidase and peroxidase and β-1, 3-Glucanase as compared to susceptible lines.

Peroxidases are regarded as detoxifying agents for H_2O_2 and have a precise metabolic function in the defence mechanism. In present investigation, peroxidase was also observed to be higher in resistant accessions of *O. rufipogon* than the susceptible accessions. This might be due to lignification of cell walls, which assists in delaying the penetration by the nematodes as mechanism of resistance. Increase in peroxidase activity may be attributed due to infection in plants as polymerization of cinnamyl lignification alcohols to lignin is catabolized by peroxidase lignification leading to disease resistance (Bhau et al., 2016). Pathogen infection results in overproduction of reactive oxygen species such as superoxide anion, singlet oxygen, hydrogen peroxidase and hydroxyl radical which are toxic (Sreedhar et al., 2013). Mahfouz et al. (2012) also reported enhancement in level of peroxidase after nematode infestation. Shamshad et al. (2024) also demonstrated that brown leaf spot resistant and moderately resistant rice genotypes have higher concentrations of the peroxidase enzyme. The findings imply that the peroxidase was crucial in the defense against brown spot disease.

Increase of PAL and TAL content was observed more in resistant accessions as compared to susceptible accessions of *O. rufipogon*. This enzyme plays a key role in the phenylpropanoid pathway, which involves the biosynthesis of polyphenols, flavonoids, and lignin precursors (Barros et al., 2016). Lignin is a component of the cell wall and vascular tissues. It confers mechanical resistance to cells, reducing nematode penetration (Ji et al., 2015; Gheysen and Jones 2006) and plant exposure to degradative enzymes released during the infection process (Gheysen and Jones 2006; Wuyts et al., 2007). Trans cinnamic acid, the product of PAL are lignin precursors and co factors of IAA oxidase and hence play a significant role in resistance reaction (Mishra and Mohanty, 2007). Studies have shown that plants resistant to *M. graminicola*, as well as rice plants treated with elicitors, deposit and accumulate lignin in the endoderm of cells surrounding the nematode feeding site, affecting nematode nutrition (Ji et al., 2015; Galeng Lawilao et al., 2018; Zhan et al., 2018). This process explains not only the reduction in J2 penetration in treated plants, but also the delay in nematode development. Umamaheswari et al. (2005) discovered that the defence enzymes PAL were more active in plants that had been treated with *M. incognita* when compared to plants that had not been treated. Ashfaq et al. (2021) also demonstrated that PAL activity was higher in leaves of brown leaf spot resistant genotypes and subsequently reduced as the resistance level decreased.

The increase in protein concentration caused by nematode infestation could be owing to the creation of novel enzyme proteins in infected plants, or it could be due to nematode contributions. Bisen et al. (2015) also observed that higher amount of soluble protein in rice leaves resulted lower disease incidence of *D. oryzae.*

4. CONCLUSION

The present study provides compelling evidence that biochemical defense mechanisms play a crucial role in conferring resistance against *M. graminicola* and *D. oryzae* in *O. rufipogon* accessions. Resistant genotypes exhibited significantly higher activity of defense-related enzymes-phenylalanine ammonia lyase, tyrosine ammonia lyase and peroxidase—as well as elevated levels of total phenols, ortho-dihydroxy phenols and total soluble proteins in comparison to susceptible accessions under both single and combined pathogen inoculations. The biochemical response was more pronounced in resistant accessions under combined pathogen stress, although a general decrease in all biochemical parameters was observed compared to single pathogen infection, indicating a complex and possibly competitive interplay between defense pathways activated by nematodes and fungi. These findings underline the importance of biochemical markers as indicators of resistance and offer valuable insights for breeding programs aimed at developing rice cultivars with durable and broad-spectrum resistance. The wild rice species *O. rufipogon* with its robust biochemical defense mechanisms, represents a promising genetic resource for introgressions resistance traits into cultivated rice varieties.

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Authors' Contributions

Anupam Sekhon and Narpinderjeet Kaur Dhillon jointly planned and executed the research work. Anupam Sekhon carried out data collection and statistical analysis. Narpinderjeet Kaur Dhillon supervised the entire study and critically reviewed the manuscript. All authors contributed to manuscript writing and approved the final version.

Conflict of Interest

Authors do not have any conflict of interest to declare.

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