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Foxtail Millet Lipoxygenase Activity in Response to *Pyricularia setariae* Causing Blast Infection

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ABSTRACT

Foxtail millet is an important staple food having good nutritional values. The fungus Pyricularia setariae causes Blast infection in foxtail millet leading to the crop loss. Lipoxygenase (LOX) activity is essential for a plant in growth, resistance to infections, and stress conditions. The present study focuses on LOX activity in foxtail millet seedlings during the course of germination and infected condition. The resistant variety of foxtail millet seedlings was exhibiting more LOX activity than susceptible seedlings, and pH 6.5 was optimum for the LOX activity. LOX activity was more in foxtail millet leaf when compared with root and stem. LOX activity was more in germinating seedlings on the day three. One-fold increase in LOX activity on infection with P. setariae causing blast infection was observed in resistant seed varieties of foxtail millet.

Key words: *Foxtail millet, Lipoxygenase, Seedlings, Pyricularia setariae, Blast infection.*

1. INTRODUCTION

Foxtail millets (*Setaria italica*) are one of the important grain crops having diverse varieties being cultivated in arid regions from ancient times in various parts of the world [1]. It is a model crop for studies on plant stress-related genes [2]. It is cultivated as feed for birds and cattle. Foxtail millet is higher in nutrition, rich in vitamins, and minerals. As it has good nutritional value, it is gaining importance for human consumption. It is an alternative food crop in drought conditions [3]. The incidence of drought is increasing every year. Fungal infections cause major crop loss in millets. Blast is one of the most serious diseases reported infecting foxtail millet. Blast disease causing pathogen *Pyricularia setariae* readily infects *S. italica* [4] and Poaceae family crops [5] leading to the production losses which can vary from very low to almost 100% [6]. The infection occurs at various stages of plant growth such as flowering, fruiting, post-harvest, pre-emergence, seedling, and vegetative growing stage. It forms circular leaf spots on the host plant. The disease in severe form causes much damage to crop [7]. These fungi can infect the crop at any stage of the growth leading to the damage of crop, grain quality, and production [8].

Lipoxygenases (LOXs; EC 1.13.11.12) have been hypothesized to inhibit many plant pathogens [9]. LOX metabolites act directly on the fungal pathogens and significant in plant resistance. LOXs are enzymes catalyzing peroxidation of polyunsaturated fatty acids forming hydroperoxides. For LOX to form hydroperoxides, the polyunsaturated fatty acid must contain cis, cis 1, 4-pentadiene moiety. The hydroperoxy polyunsaturated fatty acids, synthesized by the action of LOXs, are substrates for a series of other enzymatic reactions which lead to the synthesis of a group of biologically active compounds collectively named oxylipins [10]. The 9- or 13-hydroperoxides are further converted to different compounds by the action of other enzymes (hydroperoxide lyase, allene oxide synthase, divinyl ether synthase, reductase, and peroxygenase) belonging to different branches of the LOX pathway. The molecules synthesized by these enzymatic reactions display a wide variety of physiological roles in plant development and response to biotic and abiotic stresses [11,12].

The LOX activity was tested in many plant species. Due to the importance of LOX, it is the interest of study for scientists in various plant species. In the present study, the pH specificity of LOX, tissue specific expression of LOX, LOX activity levels in resistant, and susceptible Foxtail millet seeds during the course of germination and increased LOX activity during infection are reported.

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2. EXPERIMENTAL

2.1. Plant Material

Resistant and susceptible varieties of foxtail millet to fungal infections such as Blast and Downy mildew diseases were collected from ICRISAT, Patancheru, Hyderabad (Table 1), Regional Agricultural Research Station, Acharya N.G. Ranga Agricultural University, Nandyal-518 503, Kurnool District, Andhra Pradesh (Table 2), and Indian Council of Agricultural Research, Acharya N.G. Ranga Agricultural University, Krishi Vigyan Kendra, Utukur, Kadapa, Andhra Pradesh (Table 3).

2.2. Seed Germination and LOX Assay

Resistant and susceptible varieties of foxtail millet seed varieties were surface sterilized with 1% sodium hypochlorite for 5 min followed by washing three times with sterile distilled water to remove the surface borne microorganisms. Each foxtail millet variety weighing 25 g of seeds was soaked for 30 min in distilled water. These seeds were later allowed to germinate in germination towels and kept under constant light at 25°C until germination. The germinated seedlings were harvested at 48 h interval for 11 days. Harvested seedlings were used for extraction of LOX.

2.3. Preparation of Crude Extract for LOX Assay

A 20% crude extract of seed varieties was prepared by homogenizing the harvested seedlings in 100 mM potassium phosphate extraction buffer pH 7 containing 2 mM sodium metabisulfite, 1 mM EDTA, 1 mM ascorbic acid, 2 mM sucrose, and 1 mM PMSF in a pre-chilled mortar and pestle. The homogenate was passed through four layers of cheese cloth and centrifuged at 10,000 rpm for 30 min at 4°C. The resulting supernatant was used for the assay of LOX activity. All chemicals used were AR grade MERCK make.

2.4. LOX Activity Assay

LOX activity was measured spectrophotometrically using UV-VIS spectrophotometer. Typical reaction mixture contains 2.9 ml of assay buffer and 100 µl of enzyme. The sample was adjusted to zero absorbance by keeping the above mixture as a reference. The reaction was initiated by the addition of 10 µl of either 80 µM linoleic or α-linolenic acid as substrate. The reaction was allowed for 2 min by monitoring the formation of conjugated dienes at 235 nm in UV-visible spectrophotometer. LOX activity was measured and calculated by the following Equation 1 [13]:

$$\text{LOX activity} = \frac{\text{Volume of reaction mixture} \times \text{Absorbance difference per minute}}{\epsilon \times \text{Volume of enzyme in ml}} \quad (1)$$

Where Є (molar extinction coefficient of hydroperoxide)=27,500.

Definition of enzyme unit: One unit of LOX activity is defined as one µ mole of hydroperoxide formed per minute.

2.5. Foxtail Millet LOX pH Specificity

One resistant (ISC 1575) and one susceptible varieties (ISC 1118) of foxtail millet seed varieties were taken and surface sterilized, and seeds were soaked in distilled water for 30 min. These seeds were allowed to germinate in germination towels at 25°C until germination. The germinated seedlings were harvested after 24 h. Harvested seedlings were used for extraction of LOX. Crude extract for LOX assay was prepared, and LOX activity was measured at pH 5, 6, 6.5, 7, 8, and 9. LOX activity was measured spectrophotometrically [13] using UV-visible spectrophotometer.

2.6. Screening for LOX Activity at pH 6.5 in Different Cultivars

All the seed varieties were screened for LOX activity by LOX activity assay at pH 6.5. All the seed varieties were surface sterilized. These seeds were allowed to germinate in germination towels at 25°C until germination. The germinated seedlings were harvested at 48 h interval for 11 days. Harvested seedlings were used for the extraction of LOX. Crude extract

Table 1: Foxtail millet seed varieties from ICRISAT, Patancheru, Hyderabad.

ISc No.	Alternate accession identifier	Origin	Remarks
375	Konidhan	India	Resistant to blast
1181	EC 130490	China	Resistant to blast
1258	EC 131260, WIR 1548	Russia	Resistant to blast
1547	Chung won	Korea, Republic	Resistant to blast
1575	Chung wani2	Korea, Republic	Resistant to blast
1581	Chung wan2	Korea, Republic	Resistant to blast
1118	NESE 56-1; 3850	Syria	Susceptible to blast
1286	EC 134263/PI 179491	Turkey	Susceptible to blast

Table 2: Foxtail millet Seed varieties from RARS Nandyal, Andhra Pradesh.

No	Alternate accession identifier	Remarks
SIA 326	Prasad	Blast susceptible
GS-667	-	Downy mildew susceptible
ISc-1488	-	Blast resistant
RFM-84A	-	Downy mildew resistant

Table 3: Foxtail millet Seed varieties from Andhra Pradesh state seeds development corporation limited, Kurnool, Andhra Pradesh and Indian Council of Agricultural Research, Acharya N.G. Ranga Agricultural University, Krishi Vigyan Kendra, Utukur, Kadapa, Andhra Pradesh.

No	Alternate accession identifier	Remarks
SiA 3085	-	Resistant to Blast and Downy mildew diseases
SiA 3088	Surya Nandi	Resistant to Blast and Downy mildew diseases. Tolerant to drought

for LOX assay was prepared, and LOX activity was measured on the day 1, 3, 5, 7, 9, and 11. LOX activity was measured spectrophotometrically [13] using UV-visible spectrophotometer.

2.7. Isolation of Pathogen

Blast-infected foxtail millet in fields of Kadapa region was identified. Disease-infected leaves and plants were collected in moist paper towels for the isolation of *P. setariae*. Small bits of sterilized infected host tissue (fox tail millet) placed on fungal growth medium incubated at 25°C for 3-5 days. Mycelia growth indicates that the disease is due to isolated fungus. We got *P. setariae* culture from ICRISAT which was maintained for identification of pathogen. Infected host tissue from the advancing margin of the lesions was selected and cut into small pieces (2-5 mm) containing both the diseased and healthy tissue and kept in sterile Petri dishes containing 1% sodium hypochlorite solution for about 1 min. Pieces were transferred to Petri dishes containing sterile-distilled water and washed thoroughly in two changes of sterile water to free them from the chemicals if any. Four sterilized pieces were taken, and *P. setariae* growth was encouraged by keeping this pieces in moist Petri plates for 24 h [14] and these pieces were placed at different distance in an oat meal agar plate which was incubated in an inverted position at 25°C and examined for 3-5 days. Bits of mycelia from the margin of the colonies were aseptically transferred to the fresh oatmeal agar slants for further study. Oat meal agar used was HiMedia make. All other chemicals used were AR grade.

2.8. Checking the LOX Activity in Resistant and Susceptible Varieties of Foxtail Millet Seedlings Inoculated with P. setariae and Comparing with Uninoculated Seedlings at Different Time Intervals during Course of Germination

We have infected the foxtail millet seeds with the fungi *P. setariae.* Resistant and susceptible varieties of foxtail millet seed varieties were surface sterilized seeds that were soaked in spore suspension containing approximately 6.5×10^4 spores/mL. These seeds were allowed to germinate in germination towels at 25°C until germination. The germinated seedlings were harvested at 48 h interval for 11 days. The seeds soaked in distilled water was grown as control seedlings. Harvested seedlings were used for the extraction of LOX. Crude extract for LOX assay was prepared, and LOX activity was measured on the day 1, 3, 5, 7, 9, and 11. LOX activity was measured spectrophotometrically [13] using UV-visible spectrophotometer.

3. RESULTS AND DISCUSSION

3.1. Seed Germination

Seedlings were observed growing on germination papers (Figure 1). 1 g of seedlings were harvested on the day 1, 3, 5, 7, 9, and 11 for measuring LOX activity.

3.2. Foxtail Millet LOX pH Specificity

The LOX activity was more at pH 6.5 among the acidic pH ranges. Among the basic pH ranges, at the pH 9, the LOX activity was more. Moreover, pH 6.5 was optimum and maximum LOX activity was observed at this pH in all the seed varieties. In addition, resistant seedlings exhibited more LOX activity compared to the susceptible variety (Figure 2).

3.3. Screening for LOX Activity at pH 6.5 in Different Cultivars

We have screened for LOX activity in all the seed varieties. LOX activity was more on day 3 and 5 compared to day 1, 7, 9, and 11 of germination. Maximum LOX activity was observed on day 3. Seedlings of resistant seed varieties (ISC 1118, ISC 1286, and SIA 326) showed more LOX activity compared to susceptible seed varieties (ISC 375, ISC 1181, ISC 1258, ISC 1547, ISC 1575, ISC 1581, and GS 667) (Figure 3). There is a significant impact of days on LOX activity and significant difference between day 1 and 3, day 3 and 5, day 5 and 7, and day 9 and 11. There was no significant difference between day 7 and 9. Based on the LOX activity values, we have selected four resistant seed varieties (ISC 1547, ISC 1575, SiA 3085, and SiA 3088) with more LOX

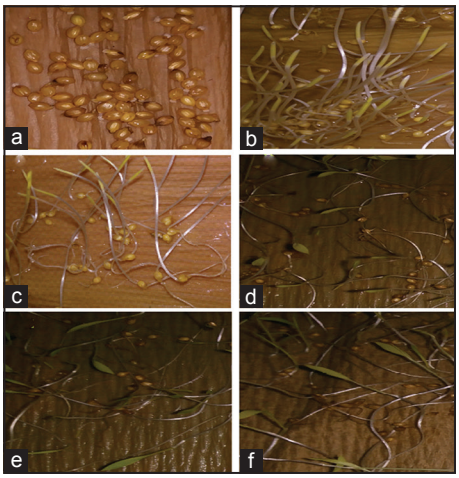

Figure 1: Germinating seedlings. (a) Day 1, (b) day 3, (c) day 5, (d) day 7, (e) day 9, (f) day 11.

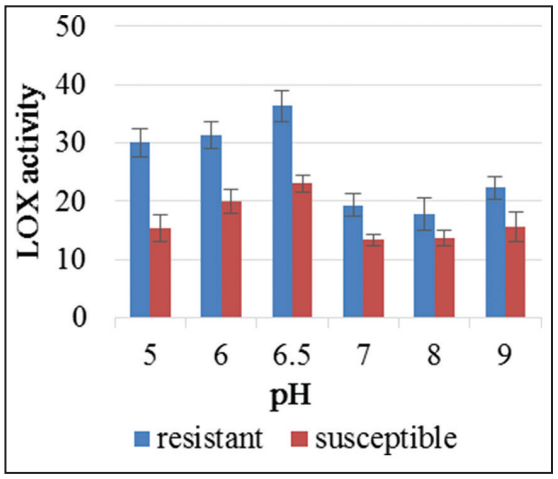

Figure 2: pH optima of foxtail millet lipoxygenase with linoleic acid (LA) as substrate. The activity was measured with 80 µM LA as a substrate in buffers (citrate pH 5, phosphate pH 6, 6.5, 7, and tris-Hcl pH 8, 9). The data represent the mean of three independent experiments ± standard deviation value. pH values for groups differ significantly with $p \leq 0.05$ with two-factor ANOVA. One unit of lipoxygenase activity = one µ mole of hydroperoxide formed per minute.

activity and three susceptible seed varieties (SiA 326, ISC 1118, and ISC 1286) with less LOX activity values for further studying the LOX activity pattern during infection with pathogen.

3.4. Isolation of Pathogen

Blast infected plants were identified and collected from field (Figure 4a). Fungal growth in infected leaf part was identified as *P. setariae* by microscopic observation (Figure 5). Fungal growth was encouraged by maintaining moist conditions (Figure 4b). Mycelia growth on the medium from the infected tissues indicated that the disease was due to isolated fungus (Figure 4c). The isolated fungus was subcultured into fresh oatmeal agar plate (Figure 6a). Pure culture of the pathogen starts growing on fresh oatmeal agar plate (Figure 6b). This culture was used for infecting the seeds. The fungus was confirmed as *P. setariae* by observing the colony, mycelium, and conidia under microscope.

3.5. Checking the LOX Activity in Resistant and Susceptible Varieties of Foxtail Millet Seedlings Inoculated with P. setariae and Comparing with Uninoculated Seedlings at Different Time Intervals during Course of Germination

LOX activity was measured in control and infected seedlings (Figure 7). LOX activity was more in resistant compared with susceptible seedlings. In addition, LOX activity was more in infected seedlings compared to the uninfected seedlings.

A one-fold increase in LOX activity was observed on day 3 of infection in infected seedlings when compared to the control seedlings; this was the maximum LOX activity observed (Figure 8). This increase in LOX activity was observed in resistant seedlings; on the other hand, the susceptible seedlings showed no difference between the LOX activities of control and infected seedlings. This increase in LOX activity was observed on infection with *P. setariae* on the day 1, 3, and 5. Increase in LOX activity was not observed on infection with *P. setariae* on day 7, 9, and 11 (Figure 9). Thus, day 3 was significant for LOX expression.

The increase in LOX activity has been observed and reported in many plant species in response to infections by bacterial, fungal, and viral pathogens. The stimulation of LOX activity was reported in pearl millet infected by *Sclerospora graminicola* causing downy mildew disease [15], leaves of tomato in response to plant pathogenic *Pseudomonads* [16], germinating pigeon pea *Cajuns cajon* seedlings infected *Fusarium udum* [17], and soybean plant in response to the attack of stem canker fungi (diaporthe phaseolorum) [18]. LOX hydroperoxides are significant in regulating aflatoxin biosynthesis, 9-S HPODE promotes and 13-S HPODE reduces aflatoxin production [19,20]. Similarly, in our study, we found an increase in LOX activity in foxtail millet resistant variety seedlings on infection with *P. setariae* causing blast infection. The pH 6.5 was optimum for the LOX activity in foxtail millet. LOX activity was more in foxtail millet leaf when compared with root and stem. LOX activity was more in germinating seedlings on day three. The resistant variety of foxtail millet seedlings is exhibiting more LOX activity than susceptible seedlings.

4. CONCLUSION

As observed in results, LOX activity was more in resistant foxtail millet varieties and LOX activity

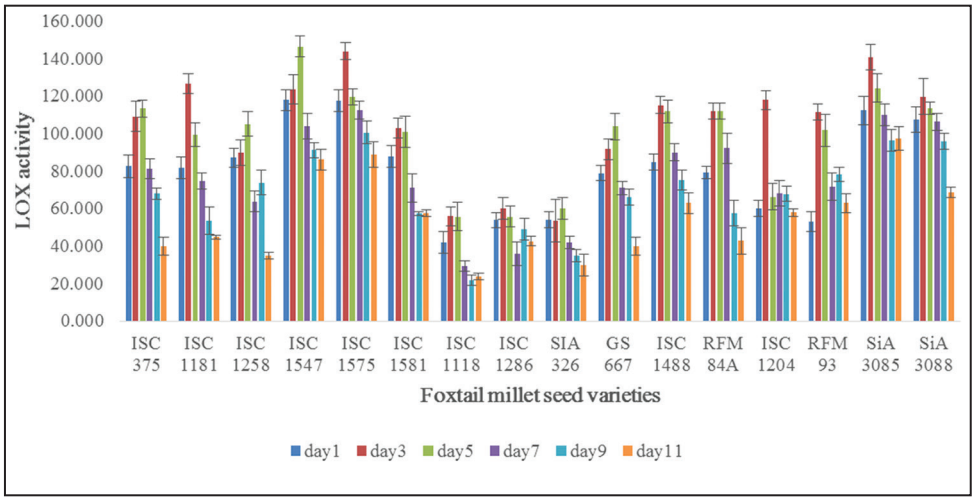

Figure 3: Lipoxygenase (LOX) activity in germinating foxtail millet seedlings with linoleic acid as substrate. Foxtail seedlings were homogenized with extraction buffer, and LOX activity was measured at 48 h interval. The data represent the mean of three independent experiments ± standard deviation value. "p" value significant with two-way ANOVA ($p \leq 0.05$). One unit of lipoxygenase activity = one µ mole of hydroperoxide formed per minute.

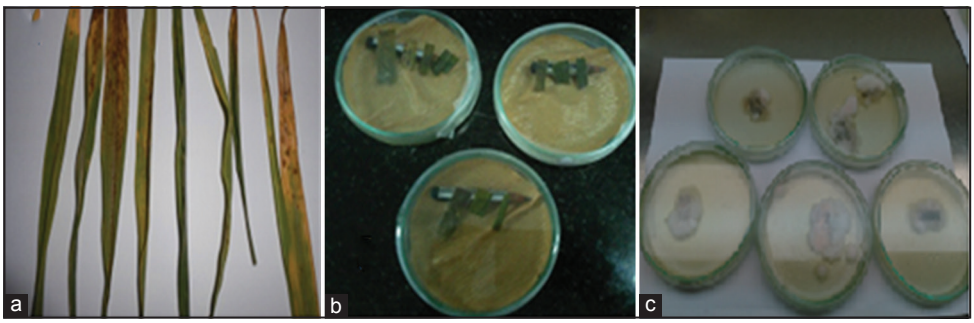

Figure 4: (a) Foxtail millet leaves collected from infected plants. (b) Infected leaf parts kept Petri plates under moist conditions for encouraging the growth of *Pyricularia setariae* (requires moist conditions for spore germination and growth). (c). Infected leaf parts from moist Petri dishes transferred to oatmeal agar plates for growth of *P. setariae* (fungal growth further encouraged by supplying required nutrients). (a) Infected leaves, (b) Moist conditions for growth, (c) Infected leaf parts on oatmeal agar.

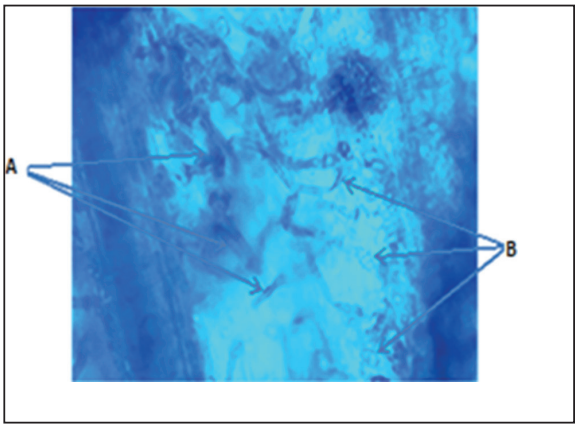

Figure 5: Microscopic (×40) observation: Growth of *Pyricularia setariae* in infected leaf. (a) Mycelium. (b) Macroconidia.

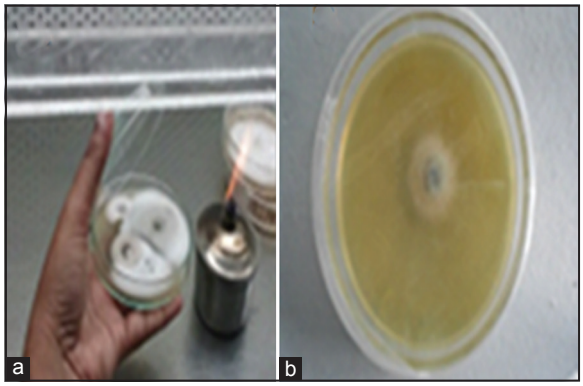

Figure 6: Fungal colony grown from infected leaf on oatmeal agar is transferred to fresh oatmeal agar plate. (a) Subculturing. (b) Growing *Pyricularia setariae* colony.

further increased in infected condition. LOX activity is essential for a plant in defense mechanism. The increase in LOX activity indicates the trigger for biochemical pathways which are involved in the synthesis of LOX metabolites that are having antimicrobial and antifungal activities. We conclude

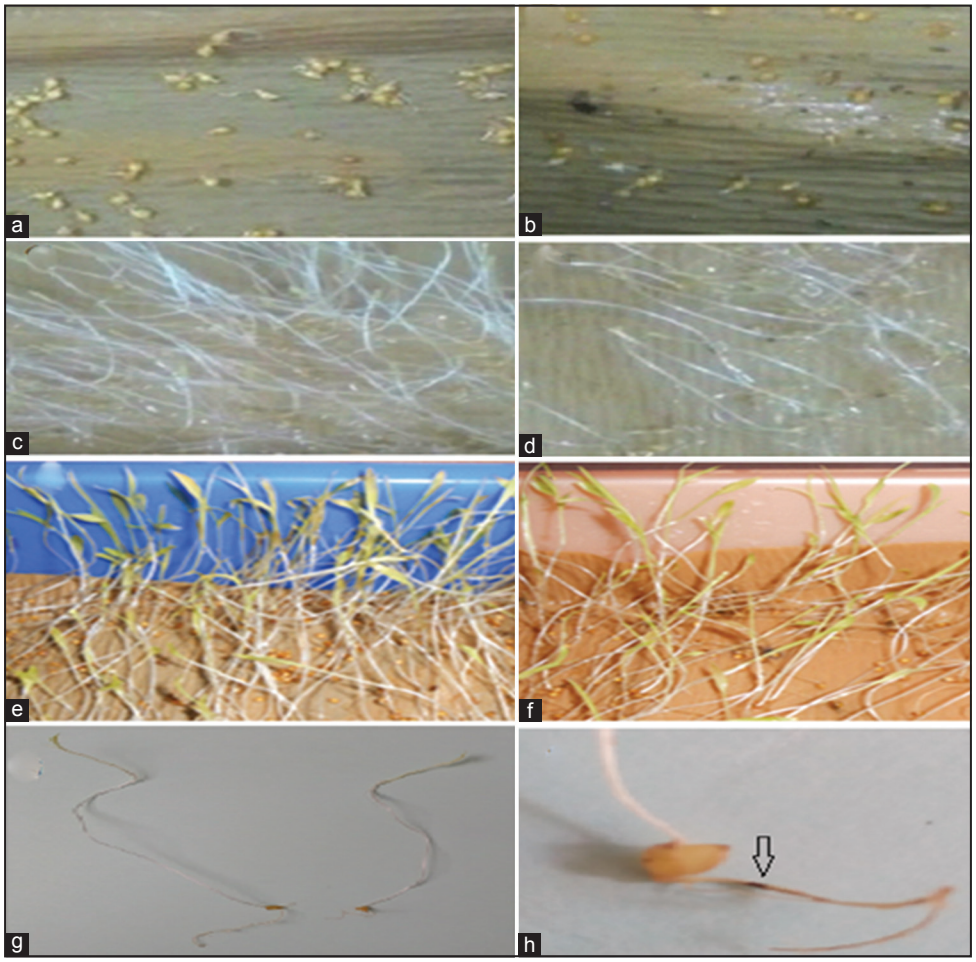

Figure 7: Growth of control and infected seedlings. (a) Control seedlings day 3. (b) Infected seedlings day 3. (c) Control seedlings day 5. (d) Infected seedlings day 5. (e) Control seedlings day 7. (f) Infected seedlings day 7. (g) Control seedlings day 9. (h) Infected seedling showing the infected region of root day 9.

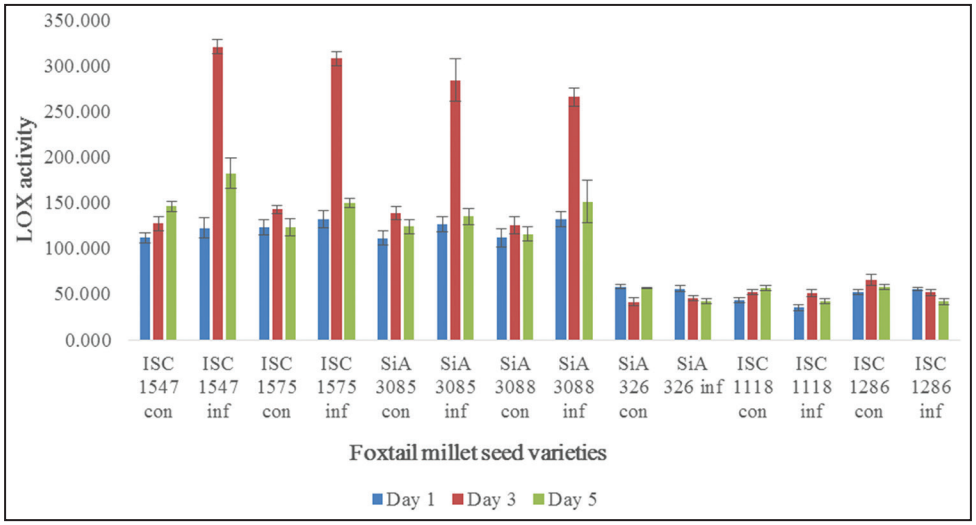

Figure 8: Lipoxygenase (LOX) activity on day 1, 3, and 5 in resistant and susceptible seedlings infected with *Pyricularia setariae* with linoleic acid (LA) as substrate. LOX activity was measured in crude extract from healthy and infected foxtail millet seedlings by spectrophotometer using LA as substrate. The data are presented as mean with standard deviation from three independent experiments with "p" value significant with two-way ANOVA ($p \leq 0.05$). One unit of lipoxygenase activity = one µ mole of hydroperoxide formed per minute.

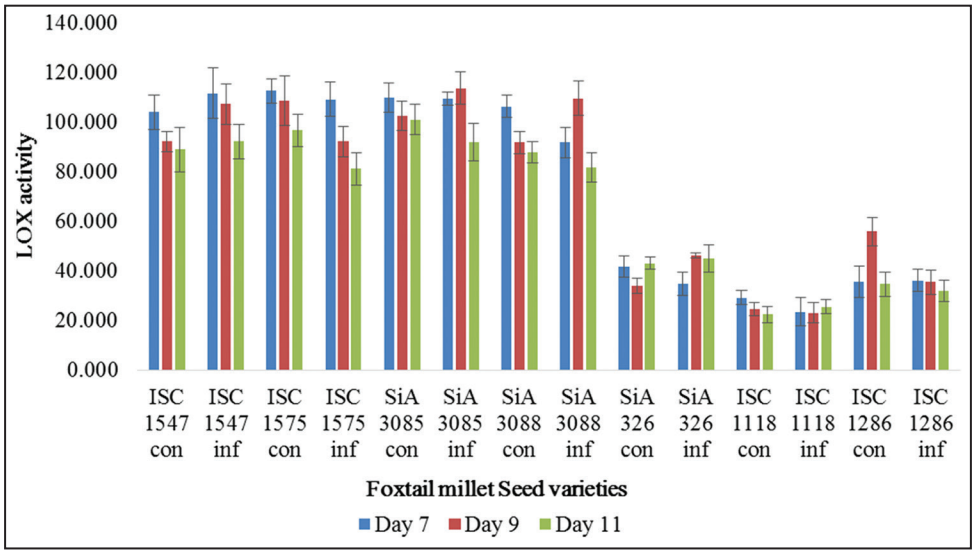

Figure 9: Lipoxygenase (LOX) activity on day 7, 9, and 11 in resistant and susceptible seedlings infected with *Pyricularia setariae* with linoleic acid (LA) as substrate. LOX activity was measured in crude extract from healthy and infected foxtail millet seedlings by spectrophotometer using LA as substrate. The data are presented as mean with standard deviation from three independent experiments with "p" value significant with two-way ANOVA ($p \leq 0.05$). One unit of lipoxygenase activity = one μ mole of hydroperoxide formed per minute.

that LOX is an essential biochemical marker for identifying disease resistance in foxtail millet.

5. ACKNOWLEDGMENTS

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***Bibliographical Sketch**

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