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ORIGINAL ARTICLE

Physiological and biochemical response of ginger varieties to virus infection

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Abstract Plant species are endowed with innate resistant machinery presumably operated through broad spectrum of defense enzymes, the products of intricate network of biochemical pathways playing vital roles in imparting resistance against numerous biotic and abiotic entities. The present study attempted to analyze physiological and biochemical alterations due to virus infection in ginger varieties viz., IISR Mahima, IISR Varada and IISR Rejatha. The results indicated that, ascorbate peroxidase and catalase activities, total protein as well as internal carbon dioxide concentration were low in healthy and high in infected plants. Whereas, acid phosphatase activity, chlorophyll (a and b), stomatal conductance, photosynthetic and transpiration rates were low in infected and high in healthy plants. Based on the observations on disease incidence in conjunction with analyses of biochemical components, it is inferred that, among the varieties studied, IISR Rejatha possess certain degree of resistance towards virus infection.

Keywords Biochemical · Chlorotic fleck · Defense enzymes · Ginger · Physiological

Introduction

Ginger (*Zingiber officinale* Rosc.) is a rhizomatous herbaceous spice representing the family *Zingiberaceae*. The modified subterranean stem i.e., the rhizome constitutes the economic part which is also extensively used for vegetative propagation. Globally, the major ginger producing countries are Bangladesh, Cameroon, China, India, Indonesia, Japan, Nepal, Nigeria, Philippines and Thailand. Wherein, India adorns the topmost position with respect to area, contributing about 46%, followed by Nigeria (19%), China (13%), Nepal (6%), Thailand and Indonesia as well as Bangladesh (3%) (FAO, 2020). In India, during 2018–19, ginger was grown in 1,73,578 ha with an annual production and productivity of 18,45,664 tonnes and 10.63 t/ha, respectively. In India, Assam, Karnataka, Madhya Pradesh, North Eastern states, Odisha and West Bengal adopts commercial cultivation of ginger (Spices Board, 2020). Ginger is considered as one among the most ancient spices with multifarious uses and Ayurveda recommends it as anti-inflammatory, antispasmodic, appetite stimulant, astringent, carminative, diaphoretic, digestive aid, diuretic, expectorant and peripheral circulatory stimulant.

Among the various economically important diseases affecting ginger, bacterial wilt, soft rot, Fusarium yellows, leaf spots (*Phyllosticta* and *Colletotrichum*) as well as storage rots are the major ones. In India, viral disease is reported to be prevalent in all the major ginger growing tracts with an incidence ranging from 10 to 90%. The prominent characteristic symptoms induced by the viruses in ginger include; formation of light green or bright yellow intravenous chlorotic flecks which subsequently merge imparting chlorosis to the entire veins. Pseudostem mottling and stunting are the other symptoms associated with the disease. Two viruses viz., ginger chlorotic fleck-associated virus 1 (GCFaV-1) and ginger chlorotic fleck-associated virus (GCFaV-2) cause the disease (Bhat et al., 2020) of which, GCFaV-1 is isometric with + ssRNA genome of about 4 kb encoding 6 open reading frames and belongs to *Tombusviridae*. While GCFaV-2 belonging to

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Ampelovirus genus and family, *Closteroviridae* have lengthy filamentous particles (approximately 1400 to 2200 nm) which contain + ssRNA of 17 to 18 kb coding up to 13 proteins (Martelli et al., 2012; ICTV, 2019).

Plants are endowed with diverse pre- and post-infection defense barriers/pathways interfering with pathogenesis (Jones & Dangl, 2006). The prominent consequences of plant-pathogen interaction are induction and accumulation of antioxidative enzymes associated with signaling and synthesis of defense compounds implicated in imparting resistance which also can be used as biochemical markers to identify resistant sources. Acid phosphatase, polyphenol oxidase, superoxide dismutase and peroxidase were employed as biochemical markers to analyze variability among ginger accessions representing diverse geographical regions of India (Sasikumar et al., 2000). Similarly, peroxidase isozyme patterns were used to examine diversity among ginger cultivars and to deduce correlation with bacterial wilt resistance in China (Chengkun et al., 1995). The current understanding on host-virus interactions and virus-induced biochemical as well as physiological alterations are limited in ginger. Hence, the present investigation was undertaken to elucidate virus-induced variations on physiological and biochemical parameters such as acid phosphatase, ascorbate peroxidase and catalase enzyme activities, chlorophyll (a and b), internal carbon dioxide concentration, photosynthetic rate, stomatal conductance, total protein as well as transpiration rate in healthy and infected categories of varieties viz., IISR Mahima, IISR Varada and IISR Rejatha.

Materials and methods

Experimental site and materials

The present study was undertaken at ICAR-Indian Institute of Spices Research (ICAR-IISR), Kozhikode, Kerala, India during 2017. The experimental materials comprised of three varieties viz., IISR Mahima, IISR Varada and IISR Rejatha. The ginger varieties were planted in growbags (40 cm × 24 cm × 24 cm) and maintained under field conditions. The planting was undertaken on 29 April, 2017 and the growbags were maintained in an area measuring 120 m^2 (280 plants in each variety). The plants were maintained under uniform shade (60%) and recommended crop production practices were followed with timely plant protection measures to manage major insect pest (shoot borer) and diseases (soft rot and leaf spot).

Per cent disease incidence

The disease incidence was documented in three varieties viz., IISR Mahima, IISR Varada and IISR Rejatha, each planted in 280 growbags during June to September, 2017 and per cent disease incidence was computed employing the formula: number of symptomatic plants/total number of plants × 100. The chlorotic streaks manifested on the foliage were categorized into mild, moderate and severe based on the severity of symptom expression. The number of plants showing symptoms in each category during different months were recorded. The cumulative number of plants (obtained by adding number of symptomatic plants in different categories) considered as diseased/infected were used to calculate per cent incidence. In the present study, 6th fully expanded leaf from tip representing healthy (Fig. 1a) and infected (Fig. 1b) categories (in triplicates) were collected for biochemical and physiological assays.

Assay of enzyme activities

To prepare crude extract, the leaf sample (1 g) was homogenized in 1:1 (w/v) of extraction buffer [50 mM potassium phosphate buffer (pH 7.0), 1% Triton-X 100 and 7 mM 2-mercaptoethanol] at 4 °C in a pestle and mortar. The homogenate was subjected to centrifugation (12,000 rpm) at 4 °C for 20 min. The supernatant obtained served as the crude extract for estimating acid phosphatase, ascorbate peroxidase and catalase activities. The assays for various enzymes were performed in a cold room maintained at 4 °C.

Assay for catalase

Catalase (EC.1.11.1.6): The reaction mixture contained 2.5 mL of 50 mM phosphate buffer (pH 7.4), 1% hydrogen peroxide (0.1 mL) and crude extract (50 µL) diluted to record the measurements within linear range of the analysis. The reduction in H_2O_2 was followed as a decline in the absorbance at 240 nm (Maehly & Chance, 1959).

Assay for ascorbate peroxidase and acid phosphatase

Ascorbate peroxidase (EC.1.11.1.11): The reaction mixture (1 mL) composed of 50 mM phosphate buffer (pH 7.0) with EDTA (0.1 mM), ascorbate (0.5 mM), hydrogen peroxide (1.54 mM) and enzyme extract (50 µL). The oxidation of ascorbate succeeded with a decrease in the absorbance at 240 nm and molar extinction coefficient U = 2.8 mM^{-1} cm^{-1} was used to determine the enzyme activity (Chen & Asada, 1989). The acid phosphatase (EC.3.1.3.2) activity was determined adopting the protocol of Sadasivam & Manickam (1992).

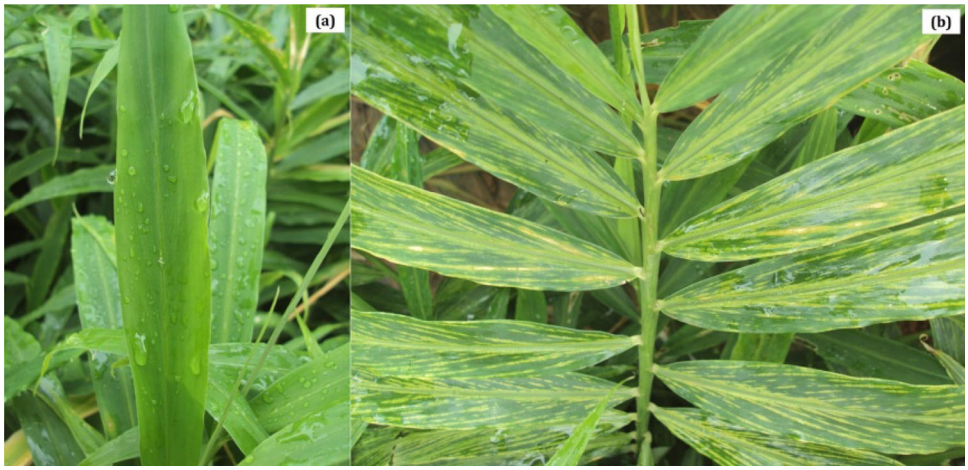

Fig. 1 Healthy (**a**) and infected (**b**) categories of ginger

Estimation of total protein

The total protein content in the leaf tissue was estimated colourimetrically employing Bradford method (Bradford, 1976) by measuring the absorbance at 595 nm wherein, bovine serum albumin served as the standard. The protein content was expressed as mg protein g^{-1} fresh weight of leaf tissue.

Estimation of chlorophyll

The chlorophyll a and b contents in the leaves of infected and healthy categories were determined adopting DMSO protocol (Hiscox & Israelstam, 1979). Briefly, the leaf discs weighing 500 mg from fully expanded leaf (6th leaf from the tip in triplicate) were placed in test tubes to which DMSO (10 mL) was added, maintained in dark for 12 h at 32 °C and the absorbance was recorded at 645 and 663 nm. The chlorophyll a and b contents were calculated following the formulae:

$$\text{Chlorophyll a}\left(\text{mg g}^{-1}\text{ tissue}\right) = \frac{[12.7(\text{OD663}) - 2.69(\text{OD645})] \times \text{V}}{1000} \times \text{W}$$

$$\text{Chlorophyll b}\left(\text{mg g}^{-1}\text{ tissue}\right) = \frac{[22.9(\text{OD663}) - 4.68(\text{OD645})] \times \text{V}}{1000} \times \text{W}$$

where; OD = Optical density at respective nm, V = Final volume of the chlorophyll extract, W = Fresh weight of the extracted tissue.

Determination of internal carbon dioxide concentration, photosynthetic rate, stomatal conductance and transpiration rate

The internal carbon dioxide concentration, photosynthetic rate, stomatal conductance and transpiration rate were documented using LCpro-SD portable photosynthesis system (ADC BioScientific Ltd, UK). Fully expanded leaf (6th leaf from the tip in triplicate) was used for photosynthetic measurements and the light intensity was maintained at 1200 µ moles m^{-2} s^{-1} using photosynthetic light control (LED) unit.

Data analysis

The assays were replicated thrice and the software SAS 9.3 version was adopted for statistical analyses.

Results

Per cent disease incidence

The disease incidence in the varieties were recorded during June to September 2017. In IISR Varada, per cent disease incidence varied from 33.57 to 85.35%, with an average of 63.92%. Whereas in IISR Mahima, the incidence ranged between 5 and 28.21% with an average of 18.74%. Compared to the aforementioned varieties, the per cent disease incidence was lowest (average 2.41%) in IISR Rejatha and within the range of 0 to 5% (Table 1).

Table 1 Per cent disease incidence in different varieties of ginger

Variety	Month				Average
	June	July	August	September	
IISR Varada	33.57	58.57	85.35	78.21	63.92
IISR Mahima	5.0	23.92	28.21	17.85	18.74
IISR Rejatha	0.0	1.78	5.0	2.85	2.41

Activity profile of catalase

The catalase (CAT) activity was found significantly higher in IISR Varada (0.61 a. u. mg^{-1} protein) followed by IISR Mahima (0.54 a. u. mg^{-1} protein) and IISR Rejatha (0.49 a. u. mg^{-1} protein) in the healthy plants which differed significantly among them (Fig. 2). There was substantial increase in CAT activity profile in infected plants compared with healthy in all the varieties. The increase in activity of CAT was pronounced in IISR Varada (24.59%) followed by IISR Rejatha (14.28%) and IISR Mahima (1.85%).

Activity profile of acid phosphatase

The acid phosphatase (ACP) activity was found to be higher (0.75 a. u. mg^{-1} protein) in both IISR Mahima and IISR Varada compared to IISR Rejatha in the healthy category. Whereas, the activity in the infected plants ranged from 0.6 a. u. mg^{-1} protein (IISR Rejatha) to 0.64 a. u. mg^{-1} protein (IISR Mahima) which significantly varied among the varieties. The activity was low in infected compared with healthy plants (Fig. 2) and the per cent reduction was higher in IISR Rejatha (17.8%), followed by IISR Varada (16%) and IISR Mahima (14.66%).

Activity profile of ascorbate peroxidase

The ascorbate peroxidase (APX) activity ranged between 0.20 and 0.27 a. u. mg^{-1} protein in the healthy plants which varied significantly among the varieties with the highest activity in IISR Varada (0.27 a. u. mg^{-1} protein). Significantly higher APX activity was recorded in the infected plants of all the varieties which ranged from 0.30 to 0.33 a. u. mg^{-1} protein compared to healthy (Fig. 2) wherein the per cent increase was maximum in IISR Mahima (55%) followed by IISR Varada (22.22%) and IISR Rejatha (20%).

Total protein

The protein content significantly varied between healthy and infected categories in all the varieties. In healthy plants, it ranged from 82.55 (IISR Rejatha) to 95.75 mg g^{-1} (IISR Varada). In infected plants, it ranged from 102.5 to 106.2 mg g^{-1} and was highest in IISR Mahima (106.20) followed by IISR Rejatha (105.75) and IISR Varada (102.5) (Fig. 3). The per cent escalation in protein content in the infected category over healthy was highest in IISR Rejatha (27.85%) followed by IISR Mahima (15.71%) and IISR Varada (6.93%).

Chlorophyll content

The chlorophyll a and b contents did not vary much among the varieties however, a substantial variation was noticed among healthy and infected categories. A significant reduction in both chlorophyll a and b contents was observed in the infected plants compared to healthy. The chlorophyll a content in the healthy plants of different varieties varied between 1.55 (IISR Mahima) and 1.75 (IISR Rejatha) mg g^{-1} fresh weight. Whereas, IISR Varada had lesser (0.75 mg g^{-1} fresh weight) chlorophyll a content compared to IISR Rejatha (0.8 mg g^{-1} fresh weight) and IISR Mahima (0.9 mg g^{-1} fresh weight) in the infected category. The content of chlorophyll b was higher in IISR Mahima (0.7 mg g^{-1} fresh weight) followed by IISR Rejatha (0.685 mg g^{-1} fresh weight) and IISR Varada (0.665 mg g^{-1} fresh weight). In the infected category, a significant reduction in chlorophyll b content was noticed, in which IISR Mahima registered the maximum (0.475 mg g^{-1} fresh weight) whereas, IISR Varada and

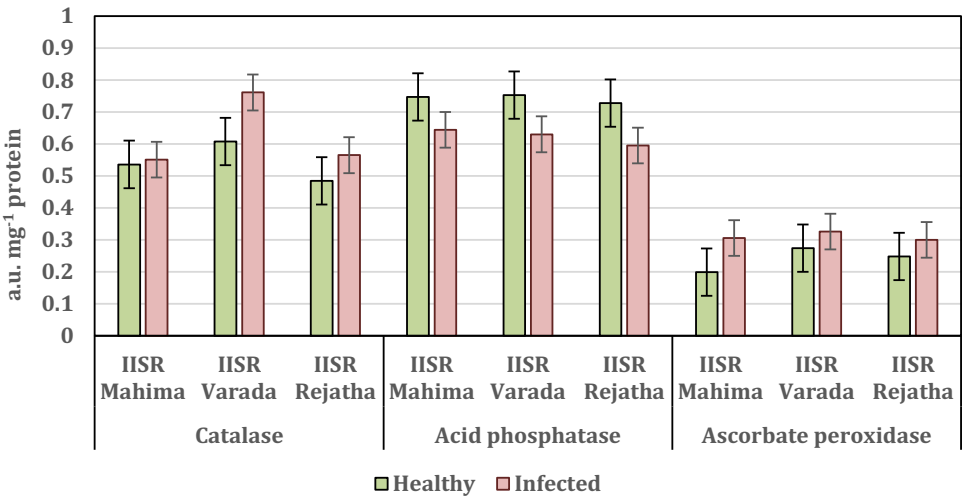

Fig. 2 Activity profiles of catalase, acid phosphatase and ascorbate peroxidase in healthy and infected categories of ginger varieties. Bars represent standard errors of the means

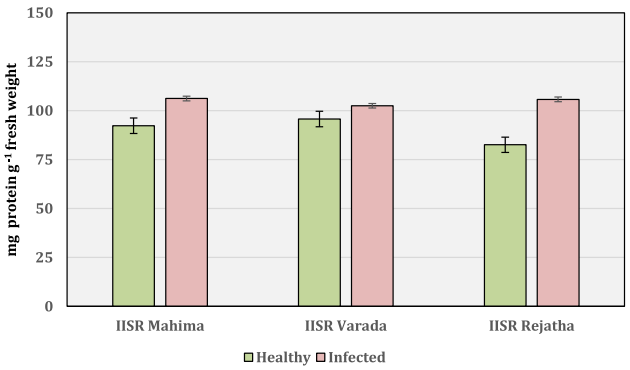

Fig. 3 Total protein content in healthy and infected categories of ginger varieties. Bars represent standard errors of the means

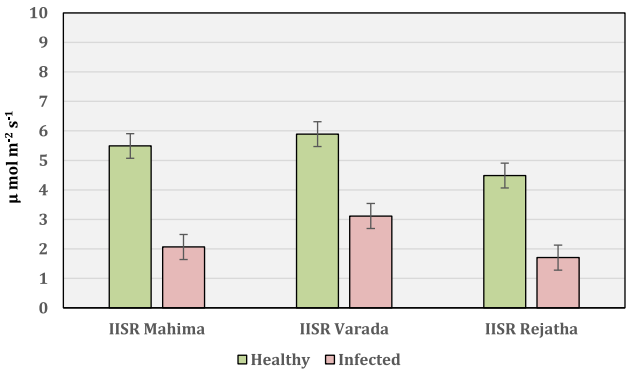

Fig. 5 Variations in photosynthetic rates in healthy and infected categories of ginger varieties. Bars represent standard errors of the means

IISR Rejatha recorded 0.36 and 0.355 mg g^{-1} fresh weight, respectively (Fig. 4). The per cent reduction of both chlorophyll a and b was higher in IISR Rejatha i.e., 55.55 and 52.77%, respectively whereas, least reduction was noticed in IISR Mahima (40% and 26.66% chlorophyll a and b, respectively).

Photosynthetic rate

The photosynthetic rate ranged from 4.48 to 5.89 µ mol m^{-2} s^{-1} in healthy category of the varieties. Significant variation among the varieties was also noticed. IISR Varada showed highest photosynthetic rate. Significantly lower photosynthetic rate was recorded in infected category of all the varieties (Fig. 5) wherein the per cent reduction was on par in IISR Rejatha (62.35%) and IISR Mahima (62.26%) and IISR Varada (48.32%) showed the least reduction compared to healthy category.

Stomatal conductance

The stomatal conductance ranged from 0.075 (IISR Rejatha) to 0.125 mol m^{-2} s^{-1} (IISR Mahima) in the healthy category. Whereas, in the infected category, there was a significant decrease which was in the range of 0.035 (IISR Rejatha) to 0.0425 (IISR Mahima) (Fig. 6). The per cent reduction was found maximum in IISR Mahima (60%) followed by IISR Rejatha (50%) and IISR Varada (44.44%).

Transpiration rate

The transpiration rate was found apparently low in the infected category of all varieties compared with healthy. The transpiration rate in healthy category ranged between 2.065 (IISR Rejatha) to 3.55 (IISR Varada) mol m^{-2} s^{-1}. Whereas, in the infected category the maximum transpiration activity was noticed in IISR Varada

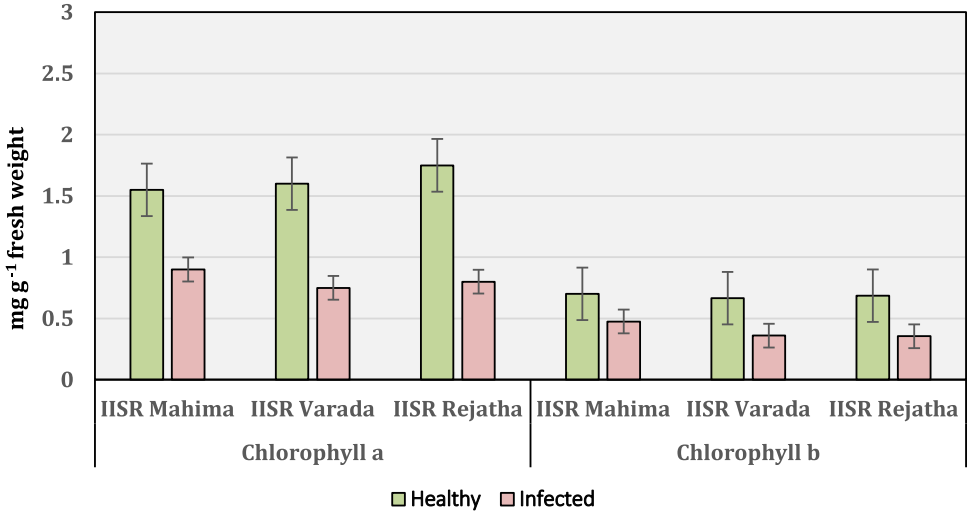

Fig. 4 Chlorophyll a and chlorophyll b contents in healthy and infected categories of ginger varieties. Bars represent standard errors of the means

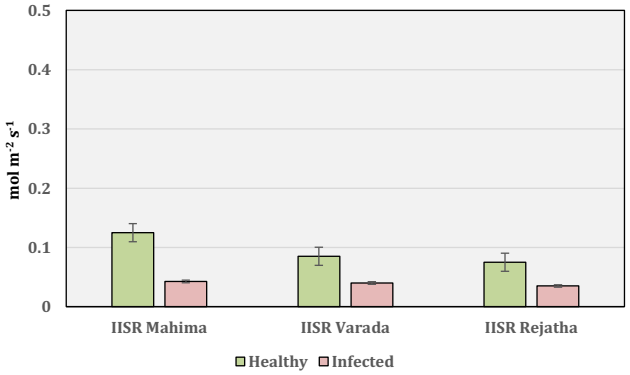

Fig. 6 Alterations in stomatal conductance in healthy and infected categories of ginger varieties. Bars represent standard errors of the means

(1.55 mol m^{-2} s^{-1}) followed by IISR Mahima (1.265 mol m^{-2} s^{-1}) and IISR Rejatha (1.15 mol m^{-2} s^{-1}) (Fig. 7). The per cent reduction in transpiration rate was highest in IISR Varada (66.6%) followed by IISR Mahima (55.23%) and IISR Rejatha (45.81%).

Internal carbon dioxide concentration

A significant variation in internal carbon dioxide concentration was observed in both infected and healthy categories among the varieties where higher values were observed in infected compared to healthy plants. It was significantly higher (277 µ mol mol^{-1}) in IISR Mahima in healthy whereas in infected category the concentration was higher in IISR Varada (294 µ mol mol^{-1}) compared to other varieties (Fig. 8). Among the varieties, IISR Varada registered the highest per cent increase i.e., 10.18% followed by IISR Mahima (4.34%) and IISR Rejatha (2.99%).

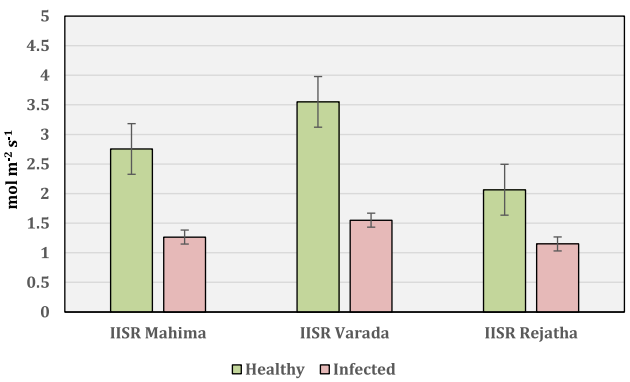

Fig. 7 Relative changes in transpiration rates in healthy and infected categories of ginger varieties. Bars represent standard errors of the means

Discussion

The analyses of physiological variations in virus infected plants would help to comprehend the cascade of events associated with disease development. Alterations in the physiological as well as biochemical processes and pathways in plants as an aftermath of virus infection have been reported by earlier researches (Radwan et al., 2010). Since enzymes mediate vital biochemical reactions in host–pathogen interaction, they could be effectively utilized as a biochemical tool to analyze the induced responses in plants manifested as symptoms (Neog et al., 2004). In the current investigation, analyses of various physiological and biochemical parameters in apparently healthy and infected categories of ginger varieties viz., IISR Mahima, IISR Varada and IISR Rejatha were carried out.

In the present study, catalase (CAT) activity was significantly higher in IISR Varada followed by IISR Mahima and IISR Rejatha in healthy plants which differed significantly and there was a marked increase in the activity profile of the enzyme in infected compared to healthy plants in all the varieties. Catalase is one among the most predominant oxygen-scavenging enzymes that mitigates oxidative stress by destroying lethal reactive species like hydrogen peroxide (Hameed & Iqbal, 2014). As seen in the present study, increased activity of catalase enzyme was also reported in banana, peanut, cotton and *Hibiscus cannabinus* infected with different viruses (Anuradha et al., 2015; Kobeasy et al., 2011; Sarkar et al., 2010; Siddique et al., 2014). In the present study, acid phosphatase (ACP) activity was found to be higher in both IISR Mahima and IISR Varada compared to IISR Rejatha in the healthy category. Whereas, the activity in the infected plants was higher in IISR Mahima. Acid phosphatase (ACP), which plays an imperative role in metabolism of phosphorus, catalyzes the hydrolysis of phosphate esters consequently releasing inorganic phosphates. Our results are consistent with that obtained by Chatterjee & Ghosh (2008) who reported reduced ACP activity in virus infected plants. In the healthy plants, ascorbate peroxidase (APX) activity varied significantly among the varieties with the highest in IISR Varada and significantly higher APX activity was recorded in the infected plants of all the varieties. Increased activity of APX observed in the present study is in accordance with previous reports in different virus-host systems (Anuradha et al., 2015; Hakmaoui et al., 2012; Hernandez et al., 2004; Rodriguez et al., 2010; Sarkar et al., 2010). The increased production of ascorbate peroxidase (APX) reinforces the scavenging system conferring oxidative stress tolerance in virus infected plants.

In general, plants suffering from pathogenic invasion exhibit higher protein content, attributed to the stimulation

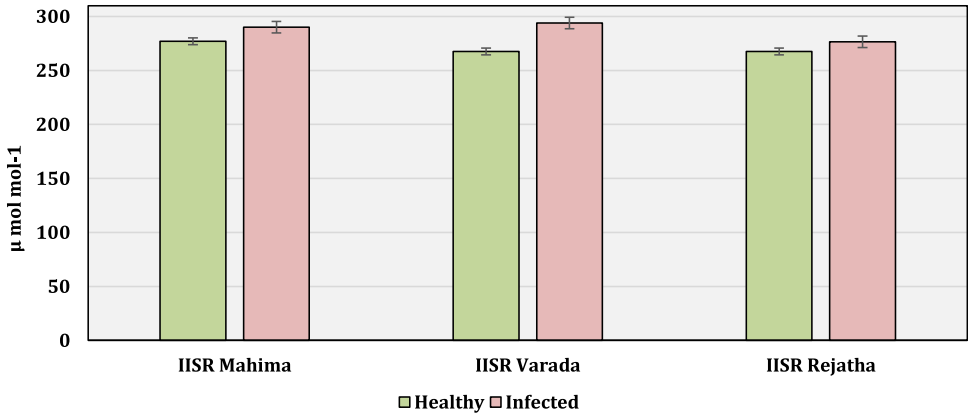

Fig. 8 Variation in internal carbon dioxide concentration in healthy and infected categories of ginger varieties. Bars represent standard errors of the means

of host defense machinery and variations induced by the pathogens. In the present study, the protein content significantly varied between healthy and infected categories in all the varieties. In infected plants, the highest was recorded in IISR Mahima followed by IISR Rejatha and IISR Varada. The per cent increase in protein content in the infected category compared to healthy was highest in IISR Rejatha followed by IISR Mahima and IISR Varada. The results are in conformation with earlier reports as exemplified with amaranthus, chenopodium and chilli infected with different viruses (Meena et al., 2008; Patel, 2004; Prakash et al., 1995). In contrast, virus infected banana and mesta plants showed significant reduction in protein content (Anuradha et al., 2015; Siddique et al., 2014). With respect to chlorophyll content, our results are in consistent with previous reports (Anuradha et al., 2015; Jabeen et al., 2017; Naidu et al., 1984; Reinero & Beachy, 1986; Zhou et al., 2004). In the present investigation, the chlorophyll a and b contents did not vary much among the varieties whereas, a considerable variation was observed among healthy and infected categories of all the three varieties. A substantial reduction in both chlorophyll a and b contents was observed in the infected plants compared to healthy. The per cent reduction of both chlorophyll a and b over healthy was maximum in IISR Rejatha whereas, least reduction was recorded in IISR Mahima. A decline in chlorophyll content in virus infected plants is attributed to the direct action of chlorophyll degrading cellular enzymes like chlorophyllase, due to the influence of virus on pigment production (Balachandran et al., 1997), altered physiological reactions including utilization of plastid proteins and the precursors for virus protein synthesis, photosynthesis and carbohydrate accumulation in the leaves. In the present investigation, significant variation in photosynthetic rate among the varieties was noticed in which, IISR Varada showed highest photosynthetic rate. Significantly lower photosynthetic rate was recorded invariably in infected category of all the varieties. A declined net photosynthetic rate could be a resultant of closure of stomata during pathogenesis. Yellowing and chlorosis (consequence of chlorophyll degradation) are the most characteristic symptoms of altered photosynthetic activities during viral infections.

Stomatal conductance is an indicator of the degree of stomatal opening and used to gauge water status in plants. In the present study, the stomatal conductance was highest in IISR Mahima and lowest in IISR Rejatha in the healthy category. Whereas, in the infected category, there was a significant reduction and the reduction over healthy was low in IISR Rejatha and high in IISR Mahima. The stomatal conductance has a direct bearing on photosynthetic and transpiration rates also. As reported by Zhou et al. (2004) and Murray et al. (2016) a substantial reduction in stomatal conductance was observed in virus infected plants of all the varieties of ginger in the present study also. Zhou et al. (2004) reported that potato virus Y infection had little influence on carbon dioxide concentration. Whereas, Goncalves et al. (2005) reported a reduction in carbon dioxide exchange rate during sugarcane yellow leaf virus infection. Nevertheless the present investigation revealed that, internal carbon dioxide concentration was evidently higher in infected plants in comparison with the healthy in all the varieties indicating that carbon dioxide might not have been utilized effectively, leading to higher sub-stomatal carbon dioxide concentration compared to healthy plants. This is also reflected in the lower photosynthetic rate of virus infected plants compared to healthy plants. The transpiration rate was found to be apparently low in the infected category of all varieties compared to healthy in the present study. In the infected category the maximum transpiration rate was noticed in IISR Varada followed by IISR Mahima and IISR Rejatha. A significant variation in internal carbon dioxide concentration was observed in both infected and healthy categories among the varieties in which it was higher in infected compared to healthy plants. Among the varieties, IISR Varada had the highest followed by IISR Mahima and IISR Rejatha. In the present study, it is observed that the physiological

parameters including the photosynthetic rate, transpiration and stomatal conductance were low in the infected category and high in healthy plants. On contrary, the internal carbon dioxide concentration was low in healthy and high in diseased plants. It is inferred that, due to the reduced photosynthetic rate, transpiration and stomatal conductance, the carbon dioxide exchange as well as utilization in the infected plants were hampered and resulted in an elevated internal carbon dioxide concentration and vice versa in healthy plants.

Conclusion

The present study revealed virus induced biochemical and physiological alterations in ginger. The activity profile of ascorbate peroxidase and catalase, total protein as well as internal carbon dioxide concentration were low in healthy and high in infected category. Whereas, acid phosphatase activity, chlorophyll (a and b), transpiration rate, stomatal conductance and photosynthetic rate were low in infected and high in healthy category. Increased activity of catalase, protein content and reduction in chlorophyll a and b, transpiration as well as photosynthetic rates and stomatal conductance in the infected category of ginger varieties are in conformation with earlier reports. However, increased activity of ascorbate peroxidase, acid phosphatase and internal carbon dioxide content were contrary to earlier reports in different host-virus systems. It is inferred from the present study that, based on physiological and biochemical activities and disease incidence, IISR Rejatha is better equipped to fight virus infection in ginger.

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Declarations

Conflict of interest The authors hereby declare that there is no conflict of interest on the publication.

Human and animal rights The present work did not comprise animals and/or human participants.

Informed consent The consent was obtained from all authors associated with the study.

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