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Efficacy of chlorophyll *a* fluorescence kinetics and JIP test for early detection of leaf-gall disease in *Cordia dichotoma*

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ABSTRACT

Gall-induced oxidative stress impairs photosynthesis and ultimately negatively affects a plant's productivity and yield. *Cordia dichotoma* is an economically important plant that suffers from galls produced by the insect *Aceria gallae.* So we investigated how plants deal with such biotic stress by studying chlorophyll fluorescence OJIP transient analysis. The results indicate the intensive variations in minimum-maximum fluorescence, electron transport, light-harvesting efficiency and density of active reaction centers. When reaction centers become inactive in severely infected leaves a significant rise in ABS/RC and TR/RC indicates the expanded antenna size of Photosystem-II which shows the plant's efforts to enhance photon absorption. But the electron transport was blocked due to OECs deactivation, remarkably altered ET/RC and phenomenological fluxes (ABS/CS, TR/CS and ET/CS). The J-curve distortion confirms blockage of electron transport towards PS-I since PQ is fully reduced and unable to grape electrons from Q_B. Leaf galls carry out noteworthy alterations in Kp, Kn, and primary and secondary photochemistry. But more severe infection causes complete obstruction for electron transport which finally diminishes performance indices (PIabs and PIcs) quantum yield of photosynthesis (ϕPo), and electron transport (ϕEo) which increases dissipation and eventually causes the death of the most severely infested leaf. Present studies reveal that measurement of F_V/F_0, PIabs, and PIcs may be used as a physiological marker for the early diagnosis of gall stress in *C. dichotoma*. Our results also suggest that repetitive detection of photosynthetic performance through chlorophyll *a* fluorescence analysis and a JIP-test can be used as potent tools to prevent plants from appearing the visible symptoms of any pathogenic infection.

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INTRODUCTION

Cordia dichotoma mostly grows in trophic or subtropical environments and is native to India and Nepal. It is an ethnomedicinal plant from the family Boraginaceae that is mostly valued for its hepatoprotective, anti-diabetic, analgesic, anti-ulcer, anthelmintic, anti-inflammatory, aphrodisiac, immune-modulator, and diuretic properties (Hussain & Kakoti, 2013; Jamkhande & Barde, 2014; Rahman & Akhtar, 2016b; Prajapati *et al.*, 2017; Bhaldar *et al.*, 2021). Leaves, Fruits and seeds include sterols, pyrrolizidine alkaloids, apigenin, coumarins, taxifolin, flavonoids (kaempferol, quercetin, and isorhamnetin), saponins, terpenes, stearic, oleic, and linoleic acids, as well as coumarins, stearic acid, and apigenin (Ganjare *et al.*, 2011; Jayaramudu *et al.*, 2011; Jamkhande *et al.*, 2013; Ragasa *et al.*, 2015; Rahman & Akhtar, 2016a; Ali *et al.*, 2017). The commercially and medicinally significant plant *C. dichotoma* is mostly harmed by gall disease in India. Galls are the abnormal growth in flora induced by microorganisms like bacteria, viruses, fungi, nematodes and arthropods. At the site of infestation, over-accumulation of auxins, cytokinin and disturbance in the jasmonic acid pathway triggers the cell cycle machinery and ultimately promotes gall formation (Patel *et al.*, 2018). The development of galls in *C. dichotoma* is currently a serious issue since it has a detrimental effect on plant photosynthesis, net primary productivity, net yielding, and the size and quality of the fruit.

The gall-inducing insects, belonging to Hymenoptera, Thysanoptera, Diptera, and Trombidiformes orders (Chireceanu *et al.*, 2015) stimulate oxidative stress, which induces cellular toxicity (Gechev *et al.*, 2006). Recent studies indicate that gall-inducing insects modulate the photosynthetic performance of host plants through the inhibition of chlorophyll biosynthesis and damaging the Photosystem-II (Bhatt *et al.*, 2022d; Bhatt *et al.*, 2023a). In the severe stage of infestation, the plants are unable to resist the disease and eventually, the leaf perishes, which negatively impacts the growth and development of the plant.

Aceria gallae form galls at the upper and lower surface of the leaves of *C. dichotoma* (Figure 1) (Xin & Dong, 1982) and belong to the Eriophyidae family (Arthropoda). Galls provide shelter to protect gall-inducing insects against environmental vicissitudes and predators (Rogerson & Mani, 1965; Stone & Schönrogge, 2003; Bailey *et al.*, 2009). Galls also act as a sink for food by drawing nutrients from remote plant organs (Larson & Whitham, 1991). But the gall formation alters biochemical and biophysical responses which negatively affect plant growth and development. When the disease spreads, leaves start to dry up and shrink, which is an obvious sign of damage in photosynthetic machinery and chlorophyll degradation (Bhatt *et al.*, 2022d; Bhatt & Soni, 2023; Liu *et al.*, 2023). Chlorophyll fluorescence kinetics is an aid as an advanced fast, sensitive, and non-destructive tool for analyzing the photosynthetic performance of leaves of the stressed. It may quickly reflect changes in light energy absorption and consumption capability of plant leaves under severe stress, making it an efficient research approach for examining the efficacy of photosynthetic systems in plant leaves under stress. The OJIP curve includes two crucial intermediary nodes, the J and I points, which hold a plethora of information on the structure and functioning of chlorophyll. As a consequence, the fluorescence curve may be separated into three primary phases, O-J, J-I, and I-P. All three phases contain both photochemical and non-photochemical information. The detailed photosynthetic activity of the plants is also derived from additional characteristics, including quantum yields, the density of active reaction centers per cross section, electron transport, and minimum-maximum fluorescence (Kalaji *et al.*, 2017; Kot & Rubinowska, 2018; Kumar *et al.*, 2021; Singh *et al.*, 2021; Bhatt *et al.*, 2022b; Bhatt & Soni, 2023).

Infestation of gall-inducing insect altered leaf lamina photosynthesis is well documented (Jiang *et al.*, 2018), Because photosynthesis is such a subtle phenomenon, diagnosing an infection before symptoms show up is one of the most effective ways to cure any plant from the disease. However, the mechanism of plants against leaf gall herbivores is not exactly known, therefore to understand the plant physiological responses against leaf galls we measured polyphasic chlorophyll fluorescence kinetics by comparing the physiology of leaves of a healthy plant.

MATERIAL AND METHODS

Study Site and Plant Material

The study was conducted to describe the degree of infestation of mites gall with the physiological strategies for survival of *C. dicotoma*. The infected plant samples were collected from the campus of Mohanlal Sukhadia University, Udaipur, India in October 2021 (25°24'54.83" N, 73°22'40.98" E). For the experiment, leaves without symptoms (NL) and with different degrees of infestation i.e. mild (MI), moderate (MO), and severe (SI) were collected from 15-20 feet long and 15-20-year-old plants of *C. dichotoma*. The control leaves (CL) with no infestation were collected from the healthy plant at Badgaon (12 km away from the study site). All institutional, national, and international guidelines and legislation guidelines were followed during the sample collection.

Analyses of Chlorophyll *a* Fluorescence Transient

Chlorophyll *a* fluorescence O-J-I-P transient was recorded by Plant Efficiency Analyzer, PEA (Hansa tech Instruments, Kings Lynn, and Norfolk, U.K.). Before measurement, infected and

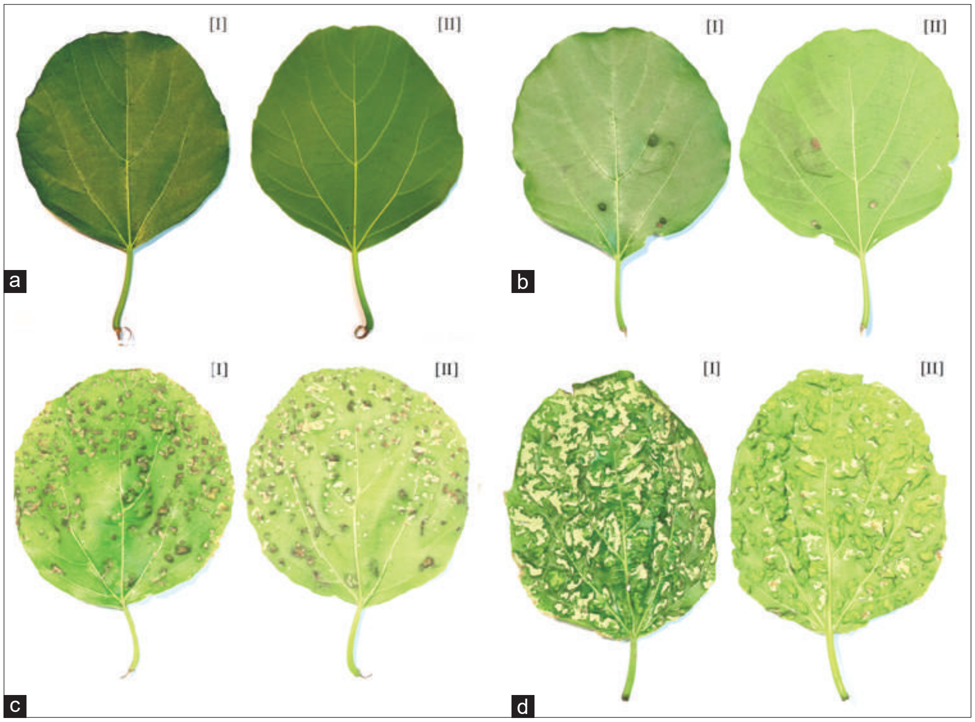

Figure 1: *Aceria gallae* infectious *C. dicotoma* plant leaf with both surface: a) healthy leaves, b) mild, c) moderate and d) severe

non-infected leaves were adapted to darkness in the room for 1 hour. Fluorescence transient was induced over a leaf area of 4mm diameter by a red light (peak at 650 nm) of 3000 $\mu mol^{-2}s^{-1}$ (sufficient excitation intensity to ensure closure of all PS-II reaction centers to obtain a true fluorescence intensity of F_M) provided by a high intensity LED array of three light-emitting diodes.

F_0, F_M and Fv/F_0

F_0 and F_M were measured as initial fluorescence at 50μs and maximum fluorescence at P peak respectively. Whereas the Fv/F_0 is the ratio of rate constants for excitation energy used by reaction centers, calculated by the following formula –

$$\frac{F_V}{F_0}=\frac{F_M - F_0}{F_0}$$

Densities of PS-II Active Reaction Center

Concentration of active PS-II RCs (RC/CS) were quantified as per the following formula (Strasser & Strasser, 1995):

$$\frac{RC}{CS}=\Phi Po \times\left[\frac{V_j}{M_O}\right]\times F_M$$

V_J and V_I

V_J and V_I are relative variable fluorescence at the J and I-steps respectively and calculated as:

$$V_J=\frac{F_{2ms} - F_O}{F_M - F_O}$$

$$V_I=\frac{F_I - F_0}{F_M - F_0}$$

Measurement of Specific Energy Fluxes

Specific activities of the active PS-II reaction center *i.e.* ABS/RC (antenna size), ET/RC and DI/RC were calculated using the following formula of JIP test (Strasser & Govindjee, 1992):

$$\frac{ABS}{RC}=M_O\times\left(\frac{1}{V_J}\right)\times(\frac{1}{PR_o})$$

$$\frac{TR}{RC}=M_O\times\left[\frac{1}{F_{2ms}-F_0}\right]$$

$$\frac{ET}{RC}=M_O\times\left[\frac{1}{F_{2ms} - F_0}\right]\times\Psi_O$$

$$\frac{DI}{RC}=\left(\frac{ABS}{RC}\right) - \ [M_O\times\left(\frac{1}{V_J}\right)]$$

Where M_O is approximated initial slope (in ms^{-1}) of the fluorescent transient, calculated as -

$$M_O=4\times(F_{300} - F_0)/(F_M - F_0)$$

Measurement of Phenomenological Energy Fluxes

Phenomenological fluxes of active PS-II reaction center i.e. ABS/CS, ET/CS, and DI/CS were calculated using the following formulas of JIP test (Strasser & Govindjee, 1992):

$$\frac{ABS}{CS}= \text{Fluorescence intensity at } 50\mu s\ (F_0)$$

$$\frac{TR}{CS}=\Phi P_O\times\left(\frac{ABS}{CS}\right)$$

$$\frac{ET}{CS}=\Phi P_O\times\Psi_O\times\left(\frac{ABS}{CS}\right)$$

$$\frac{DI}{CS}=\left(\frac{ABS}{CS}\right) - \ [\Phi P_O\times\left(\frac{ABS}{CS}\right)]$$

Measurement of Photochemical and Non-Photochemical Quenching

Maximum efficiency of PS-II photochemical quenching or (F_q'/F'_m) and non-photochemical quenching (NPQ) were calculated as per the following equations:

$$K_n=\left(\frac{ABS}{CS}\right)\times K_f\times\left(\frac{1}{F_M}\right)$$

$$K_p=\left(\frac{ABS}{CS}\right)\times K_f\times[\left(\frac{1}{F_0}\right) - \left(\frac{1}{F_M}\right)]$$

Measurement of Quantum Yield of Photosynthesis

Maximum quantum yield of primary PS-II photochemistry or ΦP_O (TR/ABS or Fv/F_M), the quantum yield of an electron from Q_A – to plastoquinone (ΦE_O or ET_O/ABS) and Maximum dissipation energy of primary PS-II photochemistry ($\Phi D_O = DI_O/ABS$) were calculated as per following equations of JIP test (Strasser & Govindjee, 1992):

$$\Phi P_O=1 - \left(\frac{F_0}{F_M}\right)$$

$$\Phi E_O=[1 - \left(\frac{F_0}{F_M}\right)]\times\Psi_O$$

$$\Phi D_O=F_O/F_M$$

Where Ψ_O is calculated as $1 - V_J$.

Conformation term for primary and secondary photochemistry

$$\frac{\varphi_O}{1-\varphi_O}=(\text{primary photochemistry})$$

$$\frac{\Psi_O}{1-\Psi_O}=1-V_J/[1-(1-V_J)$$

Measurement of Performance Indices (PI_{total})

The performance index of PS-I and PS-II was calculated as per the following formula:

$$PI_{cs}=\frac{ABS}{CS}\times\frac{1-(F_0/F_M)}{Mo/V_J}\times\frac{F_M-F_0}{F_0}\times\frac{1-V_J}{V_J}$$

$$PI_{ABS}=\frac{1-(F_0/F_M)}{M_O/V_J}\times\frac{F_M/F_o}{F_0}\times\frac{1-V_J}{V_J}$$

Data Analysis

Statistical analysis was performed using the software GraphPad Prism for Windows, version 3.0 Data were measured in triplicate sets and all data were compared by parametric tests of One-way ANOVA followed by the Tukey test method at alpha=0.05. The graphs were created by using MS Excel.

RESULTS

Biotic stress caused by A. *gallae* induced galls on the leaves surface alters the morphology (Figure 1) and physiology of the leaves of C. *dichotoma*. The chlorophyll *a* fluorescence of the healthy leaves exhibited typical O-J-I-P curves, with the altered pattern of the OJIP transient curve signifying that the photosynthetic units had been significantly impacted by environmental, biotic, or abiotic stressors. Gall development on the leaf surface changed and disrupted the regular OJIP curve (Figure 2). The leaves of infected plants show a reduction at the I position (Figure 2). In the double normalization plot (F_0 = 0.01 vs F_M=10000) the O-J-I-P curve at the J curve was highly increased in the severely infected leaves whereas a deep-down curve was formed at the I position in infected leaves except in mildly infected leaves (Figure 3), Because of this, changes were also noticed in V_J and V_I (Figures 4a & 4b). The values of V_J constantly increased with an increasing infestation of mites on the leaves of C. *dicotoma*.

In a phenomenological flux model, the intensity of the green hue of the leaf indicates a decline in total chlorophyll concentration with increasing infection (Figure 5). The variation in phenomenological energy fluxes through the cross section (CS) is represented in Figure 6. ABS/CS (Figure 6a) the light-harvesting efficiency slightly declined in MI, MO and SI leaves. But there was no significant difference was observed in ABS/CS of Cl and NL. A similar trend was recorded for TR/CS (Figure 6b) trapping per cross-section and ET/CS (Electron transport per cross-section Figure 6c) for MI, MO and SI. The ET/CS notably decreased in NL as compared to CL. Contrary to ABS/CS and ET/CS, dissipation energy per cross-section (DI/CS) was decreased with increasing the infestation (Figures 6d & 5).

Similarly, significant deviations were also found in specific energy fluxes of the active PS-II reaction center (Table 1). The progression of disease severity was accompanied by a general increase in antenna size (ABS/RC) while trapping per reaction center (TR/RC) and the electron transfer potential of active PS-II RCs (ET/RC) adequately declined from control to severely infected leaves (Figure 5). Dissipation per reaction center (DI/RC) increased NL, MI, and MO leaves while decreasing in leaves of SI. The changes in specific fluxes are also demonstrated in the specific model (Figure 5).

With a rising infestation in leaves, it is conceivable to see a decline in maximum fluorescence (F_M) and the number of active reaction centers per cross-section (RC/CS). On the other hand, the F_0 (Fluorescence at 50 μs) was higher after infestation. Meanwhile, a noteworthy decline in the primary [$\phi_o/(1-\phi_o)$] and secondary [$\Psi_O/(1-\Psi_O)$] photochemistry was observed with the severity of infection of leaf galls (Figures 7a & 7b) in the leaves of C. *dichotoma*.

A drastic reduction in Fv/F_0, performance indices (PIcs and PIabs) was also observed in NL, MO and SI (Figure 8). The radar plot showed an extreme decrease in photochemical quenching (Kp), whereas infected leaves of C. *dicotoma* showed an exponential increase in non-photochemical quenching (Kn). A noteworthy loss of quantum yield of photosynthesis (ΦPo) and electron transport (ΦEo) and a

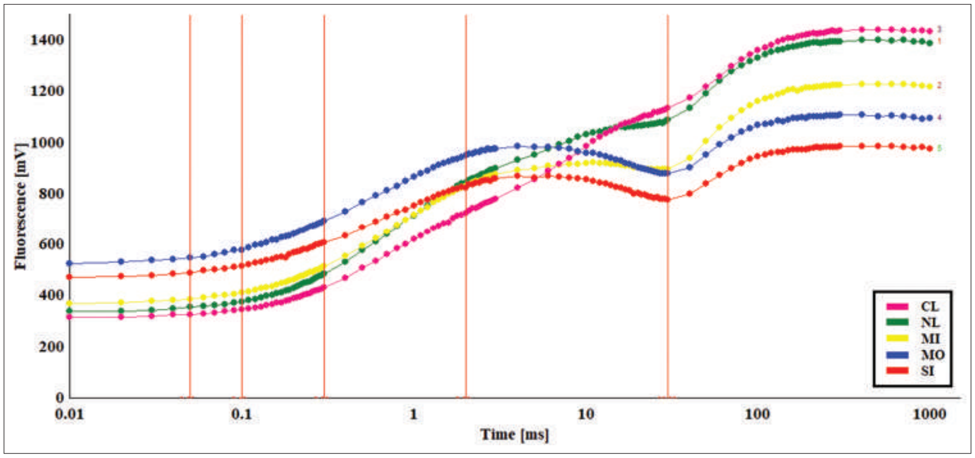

Figure 2: Chlorophyll *a* fluorescence OJIP transients of healthy and infected leaves of *C. dicotoma*

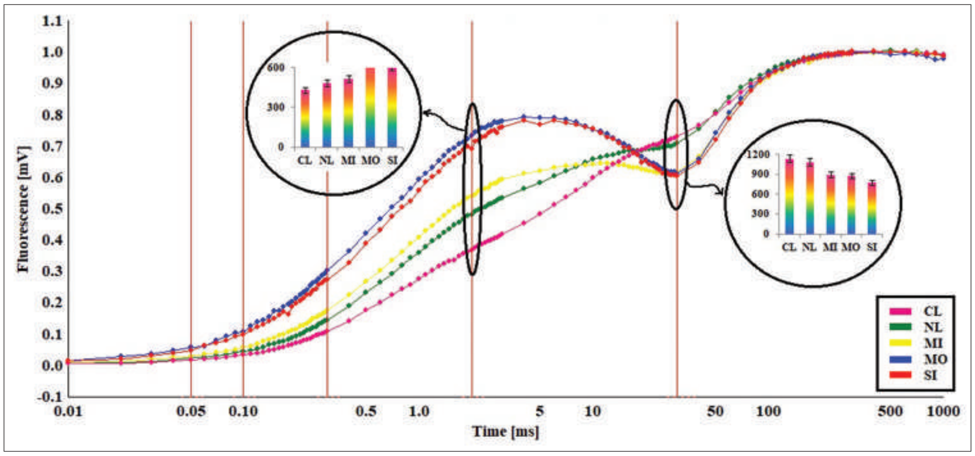

Figure 3: Double normalization curve for F_0 (0.01) and F_M (10000) showing the I depletion peak in infested leaves of *C. dicotoma*

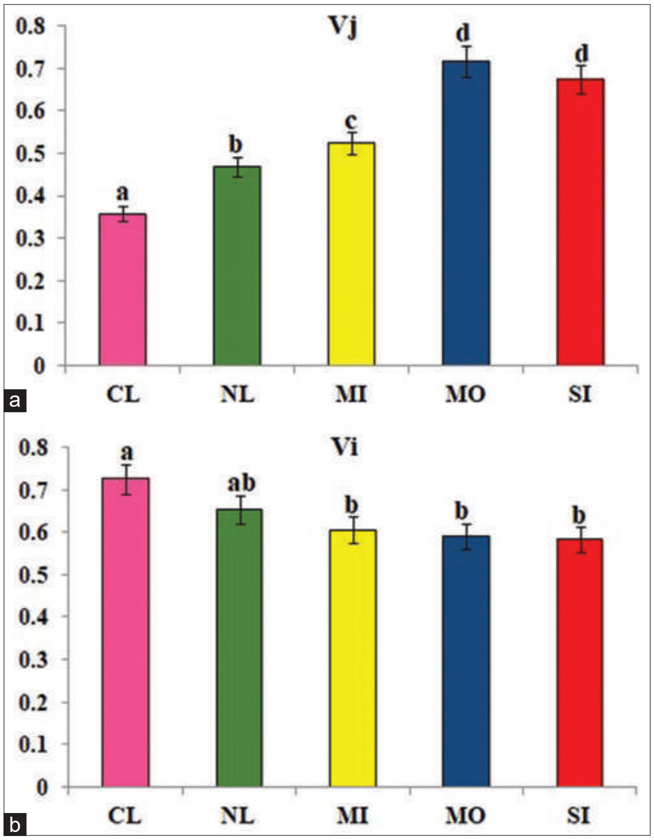

Figure 4: Bar graph represents the variation at J and I phase of OJIP transient curve with a) V_J and b) V_I parameters

rise in the quantum yield of energy dispersion (ΦDo) is also observed clearly in Figure 8.

DISCUSSION

Biotic or abiotic stresses largely affect plants' physiology and biochemistry, so it is very difficult to understand the mechanisms of plants dealing with these stresses (Bhatt *et al.*, 2023b; Shah *et al.*, 2023a, b). Gall produced by arthropods negatively affects the photosynthetic rates observed in many plants such as *Ficus religiosa* (Bhatt *et al.*, 2022d), *Machilus thunbergii* (Huang *et al.*, 2014), *Copaifera langsdorffii* (Huang *et al.*, 2014), etc. Our study reflected the major deviation in OJIP- curves while increasing infestation. Detailed analysis of OJIP-transient disclosed more information about the effects of mite galls on photosynthetic units. The OJIP curve of NL displayed a minor distortion, which is a definite indication of a disease even though the symptoms are not visible on the leaves (Figure 2). The J and I peak symptoms progressively more pronounced as the infestation progresses, significantly changing the conventional OJIP curve (Figure 3). The reduction in total chlorophyll content also results from the severity of the infestation.

The concurrent increase in F_0 (Figure 8) as compared to control shows the dissociation of PS-II reaction centers and light-harvesting complexes (LHCs) with increasing the severity of infection (Huang *et al.*, 2014; Bhatt *et al.*, 2023a), a similar pattern was also observed in *Phaseolus vulgaris* leaves when injured by spider mites (Iatrou *et al.*, 1995). F_J is an indicator for the redox state of the PQ-pool, Figure 3 shows destruction in the J curve due to the blockage of electron transport towards PS-I since PQ is fully reduced and unable to grape electrons from Q_B. This may be due to the inhibition of PQH_2-oxidase activity (Wang & Fu, 2016; Sharma *et al.*, 2021; Singh *et al.*, 2021; Bhatt *et al.*, 2022b, c). The increase in V_J is due to the accumulation of Q_A^-. Even if there are no symptoms yet, the minor tweak in the V_J of NL signals plant infection (Figure 4).

The accumulation of Q_A^- inhibit pathway for electron transport, therefore the depletion in I-peak was observed (Figure 3). The significant reduction in F_M indicated the deactivation of oxygen-evolving complexes (OECs) in MO and SI leaves (Yamashita & Butler, 1968; Neubauer & Schreiber, 1987). The high reduction in F_V/F_0 of SI indicates the depression in primary photochemistry (Figure 6) which may result from OECs deactivation (Figure 6). A constant decline in RC/CS (Figure 8) was observed in galls-affected leaves. The results denote that the inactive RCs act as energy dissipation units. The lower concentration of RC/CS causes a decrease in ABS/CS,

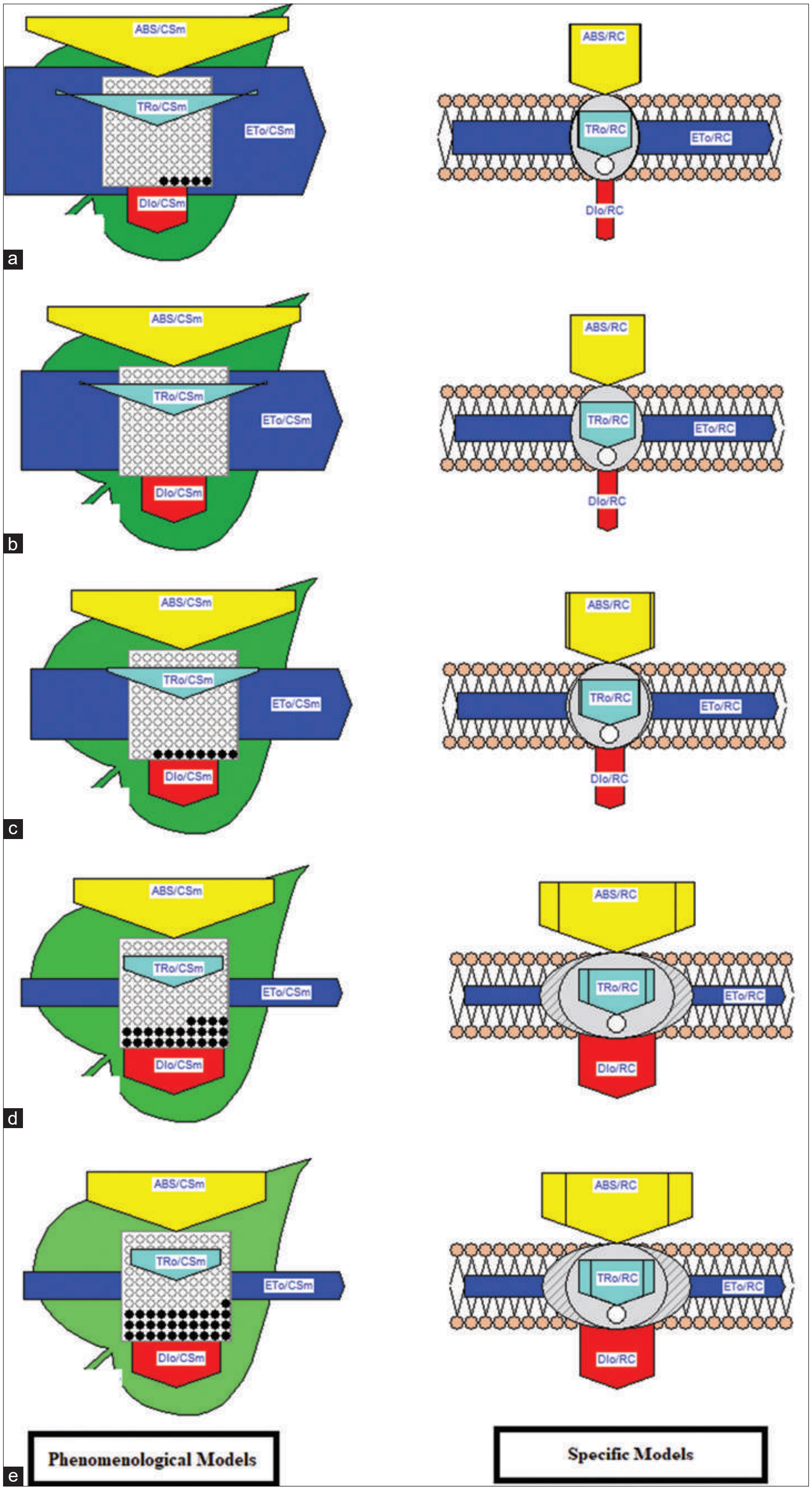

Figure 5: Leaf model and membrane model showing fluctuation of phenomenological and specific fluxes in a) control, b) healthy, c) mild, d) moderate and e) infected leaves of *C. dicotoma* respectively

Table 1: Changes in specific energy fluxes such as ABS/RC, TR/RC, ET/RC and DI/RC with increasing gall formation in leaves of *C. dicotoma*

	Specific energy fluxes			
	ABS/RC	TRo/RC	ETo/RC	DIo/RC
Control	1.312±0.068^a	1.060±0.061^a	0.679±0.015^a	0.253±0.015^a
NL	1.406±0.112^b	1.049±1.054^b	0.557±0.684^b	0.357±0.098^b
Mild infection	1.395±0.006^a	1.037±0.015^b	0.621±0.008^c	0.335±0.014^b
Moderate infection	1.621±0.190^a	1.152±0.042^c	0.551±0.047^a	0.580±0.042^c
Severe infection	2.708±0.028^c	1.4005±0.033^d	0.430±0.017^d	1.288±0.015^d

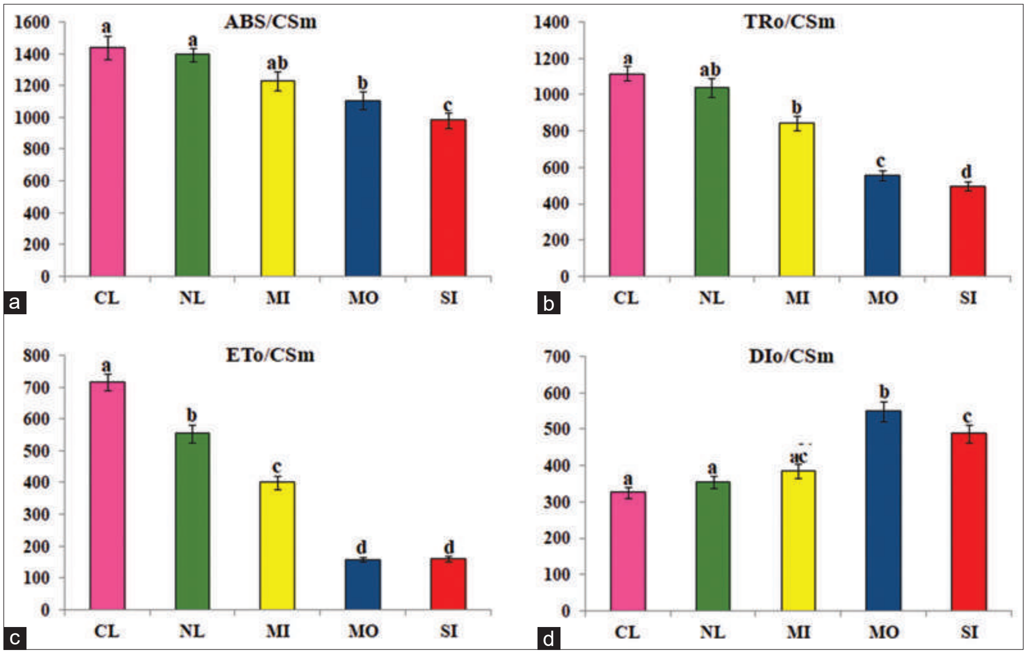

Figure 6: Changes in phenomenological energy fluxes such as a) ABS/CS, b) TR/CS, c) ET/CS and d) DI/CS with increasing gall formation in leaves of *C. dicotoma*

TR/CS and ET/CS (Figure 6a, 6b & 6c) in NL, Mo and SI leaves (Bhatt *et al.*, 2020; Kumar *et al.*, 2020; Rathore & Soni, 2020; Singh *et al.*, 2022; Soni & Swarnkar, 2017). The unused energy returned in the form of DI/CS, DI/CS gradually increased with increasing the infestation (Figure 6d) due to a lower no. of active PS-II RCs (Joly *et al.*, 2005; Eullaffroy *et al.*, 2009; Panda & Sarkar, 2012). Fic*us religiosa* leaves with gall infestation also yielded comparable results (Bhatt *et al.*, 2022d; Liu *et al.*, 2023). With the penetration of infection, the antenna size of infested leaves enlarged and attempted to absorb more energy, so the ABS/RC and TR/RC increased with the disease manifested in the leaves (Table 1). This might be a strategy for plants to survive to reduce the loss of net photosynthesis. But ET/RC lifted down in NL, MI, MO and SI leaves this enhanced DI/RC (Table 1). These may cause photoinhibition by reducing PQ-pool and forming ROS, Production of ROS-damaged protein, PS-I and PS-II (Nishiyama & Murata, 2014; Erickson *et al.*, 2015; Li *et al.*, 2018; Chotewutmontri & Barkan, 2020). Kp reduced (Figure 6) due to a reduction in RC/CS (Kumar *et al.*, 2021; Soni *et al.*, 2021; Bhatt *et al.*, 2022c; Bhatt & Soni, 2023; Sharma *et al.*, 2023b). After the appearance of symptoms on MI leaves, the number of active reaction centers increased as compared to CL.

Non-photochemical quenching (Kn) is the testimony about the degree of absorbed photons intended for heat dissipation under stress conditions (Mommer & Visser, 2005). Due to ceased ETC $[\phi_o/(1-\phi_o)]$ and $[\Psi_O/(1-\Psi_O)]$ (Figures 7a & 7b) decreases which ultimately negatively influence photosynthetic potential so a high depression was found in ϕPo and ϕEo (Henriques, 2009; Zai *et al.*, 2012) due to the damage to PS-II components (Maxwell & Johnson, 2000; Bhatt *et al.*, 2022c; Roháček, 2002; Sharma *et al.*, 2023a). The declined photosynthetic rate is correlated with photosynthesis regulatory genes. Nevertheless, performance indices must reveal the overall photosynthetic performance; PIabs reflected the index of energy conversion which significantly designated various stresses in terms of influence on RC/CS and energy fluxes (Strasser *et al.*, 2004). Therefore the reduction in PIabs and PIcs shows the fall down in overall photosynthetic performance in the most SI leaf, which finally causes the death of that leaf (Bhatt *et al.*, 2022a, b, c; Bhatt *et al.*, 2023a). Because there are more active reaction centers in MI leaves, performance indices have increased. PIabs and PIcs significantly declined in NL as compared to CL, therefore, these may be the characteristic parameter for the early detection of gall stress in *C. dichotoma*.

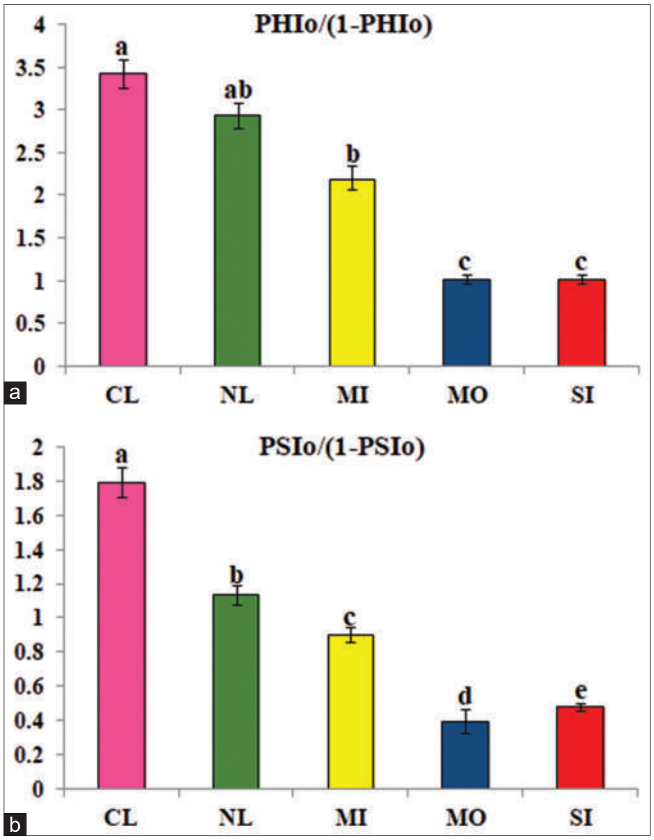

Figure 7: Graphs showing alteration in a) primary photochemistry and b) secondary photochemistry during infestation in *C. dicotoma*

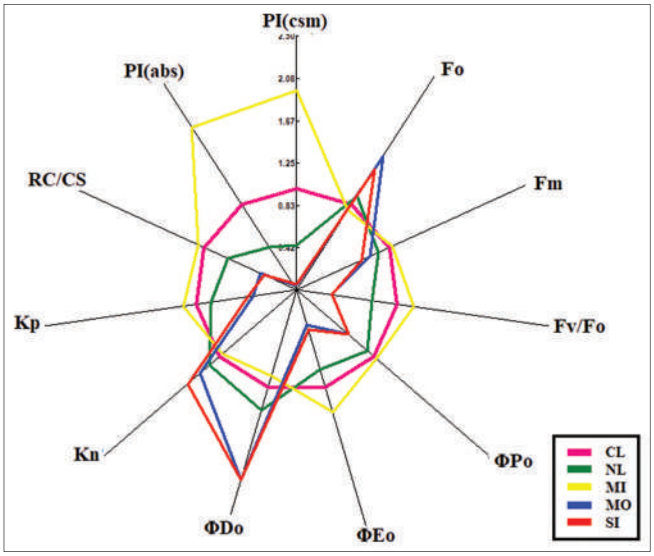

Figure 8: Radar plot showing various parameters of photosynthesis F_M, F_0, PIcs, PI(abs), Kn, Kp, ΦPo, ΦDo, ΦEo, Fv/F_0 and RC/CS

CONCLUSION

Some insects trigger cecidogenesis that causes gall formation by transcriptional reprogramming, therefore to understand physiological responses against biotic stress caused by A. *gallae*, we evaluate photosynthetic activity by measuring OJIP transients. The results of the current research concluded the overall reduction in PIcs is due to the remarkable decline in phenomenological fluxes (ABS/CS, TR/CS, ET/CS) and quantum yield (ϕPo and ϕEo). Although the plant tried to raise the photosynthesis by increasing antenna size so that ABS/RC and TR/RC were enhanced. But the ET/CS ceased due to the inactivation of PQH_2-oxidase which plays a crucial role in defense mechanisms. F_V/F_0, PIabs and PIcs may be the characteristic parameter for the rapid diagnosis of gall stress in C. *dichotoma* since they considerably decreased in NL as compared to CL. So, we can conclude that the ongoing monitoring of plant chlorophyll fluorescence can aid in the treatment of gall disease before symptoms manifest.

AUTHOR'S CONTRIBUTION

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Vipul Anjana and Upma Bhatt. The first draft of the manuscript was written by Upma Bhatt and Vipul Anjana. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. Vineet Soni supervised the whole work and corrected the manuscript.

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