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Metabolites in galls induced on the leaves of *Trewia nudiflora* (L.) (Euphorbiaceae) by *Trioza fletcheri* Crawford (Hemiptera, Triozidae)

Om Datta[1*] and Sunil Tomar[2]

[1]*Department of Zoology, M.S. College, Saharanpur247001, U.P., India.*
[2]*Department of Zoology, D.A.V. College, Muzaffarnagar 251001, U.P., India.*
Email: omarjun969@yahoo.com

ABSTRACT: *Trioza fletcheri* Crawford is a sap-sucking psyllid that induces galls on *Trewia nudiflora* leaves. Early stages of *T. fletcheri* feed on parenchyma, whereas late-stages and adults feed on phloem, causing galls which arise in an isolated, agglomerated mass and rosette form only on the abaxial surface of *T. nudiflora* leaves. The feeding action of immature stages induces changes in metabolites of host tissue and creates a nutrition sink for feeding. The biochemical study revealed that galled tissues had higher levels of metabolites (total soluble sugars, reducing sugars, total protein and free amino acids) than ungalled tissues, with average values measuring 3.4±0.09, 1.4±0.1, 0.63±0.03, 1.9±0.23, 3.0±0.72mg/gdw in ungalled leaves; 4.3±0.02, 2.9±0.3, 1.9±0.47, 3.7±0.36, 4.7±0.53 mg/g dw in young galls; 3.8±0.50, 3.7±0.3, 1.03±0.04, 2.9±0.35, 5.4±0.31 mg/g dw in mature galls; and 2.7±0.23, 2.4±0.3, 0.83±0.03, 2.6±0.34 and, 4.3±0.22mg/g dw in old galls, respectively. Enhanced activities of IAA-oxidase, α-amylase, peroxidase, and invertase were observed in galled infested leaves than in ungalled leaves, and their values were measured to be 2.45±0.53, 2.4±0.3, 0.9±0.2, and 3.7±0.5 in ungalled leaves, 2.92±0.32, 3.2±0.2, 1.9±0.5 and 4.5±0.3in young galls, 3.7±0.43, 3.6±0.4, 1.4±0.4, 4.3±0.2 in mature galls, and 2.51±0.03, 2.9±0.4, 1.4±0.4, 3.8±0.1 in old galls respectively.

KEYWORDS: Psyllid, infested tissue, biochemical changes, metabolites, enzyme activities

INTRODUCTION

Trioza fletcheri Crawford is a sap-sucking insect that belongs to the family Triozidae and subfamily Psylloidea (Bodlah *et al*., 2012). Life stages of the Psylloidea, *T. fletcheri,* include adult stage (Fig.1), egg (Fig. 2) and five immature stages (Sharma *et al*., 2013, 2014, 2015). Early stages (Fig. 3) feed on parenchyma, whereas late stages (Fig. 4) and adults feed on phloem. Gall initiation is triggered by the feeding action and salivary enzymes released by first instars (Burckhardt, 2005; Raman, 2011, 2016; Sharma and Raman, 2022). The galls are the modified, invariably symmetrical, naturally developing plant structures that arise because of messages from the inducing insects (Mani, 1964; Raman, 2011), and develop as an extension of the host plant phenotype (Weis *et al.,* 1988; Chen *et al.,* 2015). The galls provide nutrition and shelter to the inducing insects. The insect activates a perturbation in growth mechanisms and alters the differentiation processes in the plant, modifying the plant's architecture to its advantage (Raman, 2003). *T. fletcheri* induces pimples and pouches like galls

* Author for correspondence

that arise in an isolated (Fig. 6), agglomerated mass (Fig. 7) and rosette form (Fig. 8) only on the abaxial surface of *T. nudiflora* leaves.

The medicinal plant *Trewia nudiflora (L.) (Euphorbiaceae)* (Fig. 5) is an important in the Indian medicine in Ayurveda and Siddha (Balakrishnan *et al*., 2013). The root decoction of *T. nudiflora* is used as a stomachic therapy for flatulence, gout, rheumatism, cancer, particularly leukaemia and hepatobiliary affections, while, a decoction of shoots and leaves is used to treat edoema, flatulence, excess bile and sputum (Balakrishnan *et al*., 2013). It is a host for *T. fletcheri* that induces galls on its leaves (Crawford, 1924; Yang and Raman, 2007). The present study aims to describe the metabolite changes in leaf galls of *T. nudiflora* induced by *T. fletcheri.*

MATERIALS AND METHODS

Collection of samples: Samples for the study were collected from the Haridwar district, a small historic city in the state of Uttarakhand located on the banks of the Ganges River at 29.945690 latitude and 78.164246 longitude.

Biochemical analysis: For biochemical analysis, fresh samples from the same study area were collected from the uninfested and infested plant of *T. nudiflora* plant during 2019-2020. For convenience the collected samples of leaves were categorized into: (A) Ungalled leaves of uninfested plants; (B) galled leaves of infested plant with young, mature, and old galls. Fifty samples in each category were chosen for the study.

The samples were washed in distilled water and then dried in the air on Whatman's filter paper for 25-30 minutes. Gall samples were trimmed with the help of a sharp razor and residing nymphs were removed by partial slitting of the galls. A sub sample of each of ungalled leaves, gall infested leaves, young, mature and old galls was prepared and used for each biochemical assay.

The samples were ground in a mortar and boiled in ethanol (80%) to obtain an extract, which was then filtered through Whatman's (#1) filter paper.The extract was used for assaying total sugars following Plummer (1971), total phenols following Bray and Thorpe (1951), free amino acids following Moore and Stein (1948), total proteins following Lowry *et al*. (1951), reducing sugars following Miller (1972), and total soluble sugars following Dubois *et al.* (1951). Tests were repeated for 4-5 duplicates, and five values of each biochemical assay of ungalled and galled tissue were observed to obtain the mean data and standard error. Obtained values were expressed as mg g^{-1}.

pH analysis: For pH analysis,both ungalled and galled infested leaves were collected from the study area. From the gall infested leaves, young, mature, and old galls were picked. The young and mature galls were carefully opened to remove the nymphs residing in the galls. A solutionof the ungalled leaves, galled leaves, young, mature, and old galls was prepared by crushing in distilled water, and the pH value of each sample was measured using BDH paper strips and a digital pH meter (BST-PT13 manufactured by Bionics Scientific Technologies (P). Ltd, India).

Estimation of enzyme activity: One gram plant sample was crushed in 3 ml of cold sodium phosphate buffer (0.02M, pH 6.0). The concentrate was centrifuged at 12298 'G' values (Remi Refrigerated Centrifuges, C-24 Plus) for 15 min in a refrigerated centrifuge at 4^0C. The supernatant was mixed in a two fold quantity of cold acetone and allowed to incubate at 5^0C for half an hour to precipitate the proteins. The solution was centrifuged again at 4^0C for 10 min at 3600 rpm. The supernatant was disposed, while the pellet was re-suspended in 10 ml of phosphate buffer (0.02M, pH 6.4) and used as the enzyme source. The extract was used for assaying peroxidase following Birecka *et al*. (1973), Alpha-amylase following Bernfeld (1955), Invertase following Harris and Jeffcott (1974) and IAA-oxidase following Mahadevan and Sridhar (1986). The experiments were repeated four to five times to obtain the mean values with standard errors.

The experiments were conducted in randomized

design and the data expressed in average of replications were analysed statistically.

RESULTS AND DISCUSSION

The study showed that gall inducing on the leaves of *T. nudiflora* by *T. fletcheri* leads to considerable changes in major metabolites of plant's tissue.

Total soluble sugars

Higher values of total soluble sugars were recorded in galled tissues as compared to ungalled tissues. The soluble sugars were higher in young galls than in mature and old galls, with mean values of3.4±0.09, 4.3±0.02, 3.8±0.50, 2.7±0.23 mg g^{-1} dw in ungalled leaves, young, mature, and old galls respectively (Table1). The total sugar content might be higher in young and mature galls because of the enhanced metabolic activity of nymphs during feeding stress. Mukharjee *et al*. (2016) and Biswas *et al*. (2018) also reported enhanced total sugar content in mature and perforated psyllid galls of *T. tomentosa* and *T. arjuna.*.

Total reducing sugars

Enhanced value of total reducing sugars was observed in galled tissues in comparison to ungalled leaves. Highest value of reducing sugars was observed in mature galls. The mean values of total reducing sugars were recorded to be 1.4±0.1, 2.9±0.3, 3.7±0.3, 2.4±0.3 mg g^{-1} dw in ungalled leaves, young, mature and old galls respectively (Table 1). Galled tissues showed higher level of reducing sugars than ungalled leaves, which is supported by previous reports of Dsouza and Ravishankar (2014) and Kumar *et al*. (2015).

Total phenols

Total phenol content was higher in galled tissues as compared to ungalled tissues.The highest phenol content was observed in young galls, especially during early cecidogenesis, and declined later in the mature and old galls. Average values of the total phenol were 0.63±0.03, 1.9±0.47, 1.03±0.04 and 0.83±0.03 mg g^{-1} in ungalled leaves, young, mature and old galls respectively (Table1). In winters, quantity of phenol increases in the galled tissues to trap the solar heat and to maintain the optimum temperature inside the gall. Elevation of phenol compounds in psyllid galls is a common phenomenon (Balakrishna and Raman,1992). As a defence against invading pests and pathogens, plants synthesize a variety of secondary chemicals and phenols depending on their genotype (Kar *et al*., 2013). Various groups of phenolic compounds defend the plant against microbes and herbivores (Kraus and Spiteller,1997). Plants develop resistance to pathogen-caused disease when high levels of phenol are present (Mehrotra and Aggarwal, 2003). Thus, the high amounts of phenolic compounds in the galled tissue of *T. nudiflora* provide resistance to insect infestation. Dsouza and Ravishankar (2014), Mukharjee *et al*. (2016) and Mujahid *et al*. (2019) also reported higher phenol contents in psyllid galls.

Total protein

Total protein content increased in galled tissues as compared to ungalled tissues. The highest protein content was observed in young galls that declined gradually in mature and old galls. The total protein contents were 1.9±0.23, 3.7±0.36, 2.9±0.35, 2.6±0.34 mg g^{-1} in ungalled leaves, young, mature, and old galls respectively (Table1). The galled tissues had higher total protein levels than the ungalled leaf tissues, which is supported by the previous studies (Arora and Patni, 2001; El-Akkad, 2004; Scareli Santos and Varanda, 2003; Mukharjee *et al*., 2016). Plant protein synthesis play an important role in defence (Reinbothe *et al*., 1994). Higher protein levels in the leaves during gall infestation are due to enhanced secretion of defensive proteins by the host plant, which inhibits the activity of insect's proteolytic enzymes.These proteins are proteinase inhibitors that are quickly stored throughout the plant and ungalled areas as a result of insect feeding, even in those areas that are far from the early feeding location (Ananthakrishnan, 2001). Besides this, decline in protein content in mature and old galls may be due to less need of protein or the protein secretion has reached satiation in the host-plant (Raman *et al.*, 1997).

Free amino acids

The quantity of free amino acid was equal in ungalled leaves and young galls; whereas, mature galls showed the higher concentration of free amino acids. The quantity of free amino acid decreased in old gall tissue. The mean values of free amino acids measured to be 3.0±0.72, 3.0±0.72, 5.4±0.31, 4.3±0.22 mg g^{-1} dw in ungalled leaves, young, mature and old galls respectively (Table1). An increase in amino acid in galled tissues is due to the breakdown of protein into usable molecules by protease secreted by the insects' salivary glands (Miles and Lloyd,1967; Miles, 1968). In gall-inducing insects, the amino acids in galls serve as building blocks for protein synthesis (Birch, 1974). The galled leaves of *T. nudiflora* had a higher concentration of free amino acids than the ungalled leaves. The gall-inducing insects manipulate the host plants for their own advantage (Hartley and Lawton, 1992).

IAA-oxidase activity

Enhanced activity of IAA-oxidase was observed in galled tissues than in ungalled tissues and it was highest in mature galls. The mean values of IAA-oxidase were 2.45±0.53, 2.92±0.32, 3.7±0.43, and 2.51±0.03 mg in ungalled leaves, young, mature, and old galls respectively (Table1). IAA is the main auxin in higher plants, which has profound effects on plant growth and development. Both plants and some plant pathogens can produce IAA to modulate plant growth (Zhao, 2010). The high level of phenol adversely affects the IAA-oxidase activity in plant tissue, resulting in a higher level of IAA, thus leading to hyperauxinity and gall induction. A high level of IAA supports cell expansion (hypertrophy) and cell division (hyperplasia).

α-amylase activity

Increased α-amylase activity was observed in galled tissues as compared to ungalled tissues and was maximum in mature galls. The mean values of α-amylase activity were measured to be 2.4±0.3, 3.2±0.2, 3.6±0.4, and 2.9±0.4 mg m^{-1} dw in ungalled leaves, young, mature, and old galls, respectively (Table1). Enhanced activity of α-amylase in mature galls of *T. nudiflora* is triggered by the feeding stress of immatures of *T. fletcheri*, which increases the metabolic activity of galled tissues, stimulating sugar formation. The depletion of starch accumulates carbohydrates due to activated α-amylase activity and other enzymes. Increased activity of α-amylase in gall-infested leaves along with increased sugar levels was also reported by Garg and Mandhar (1975), Shekhawat (1980), Rao (1989), Purohit (1980) and Dsouza and Ravishankar (2014).

Peroxidase activity

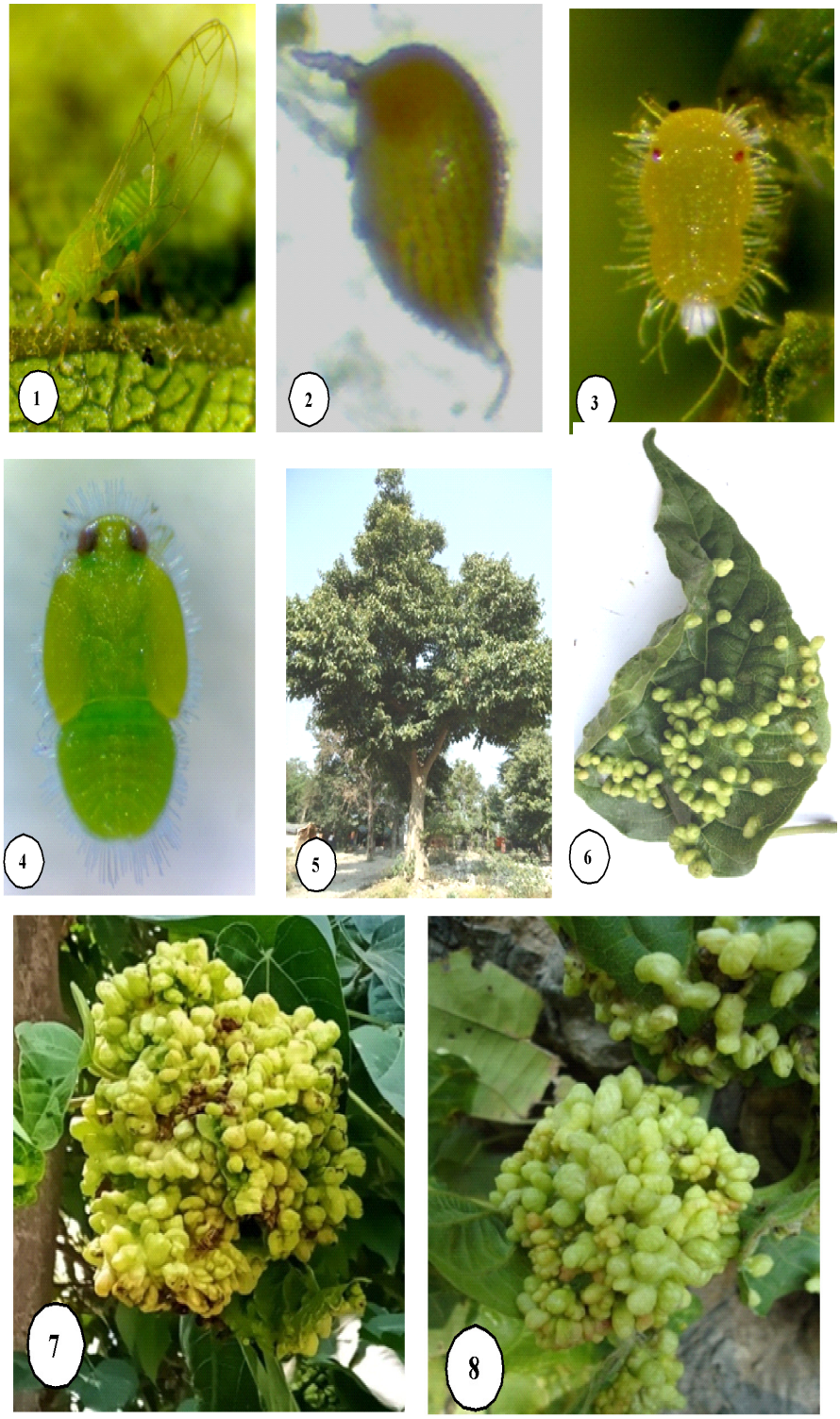
Enhanced activity of peroxidase was recorded in galled tissues as compared to ungalled leaf tissues. The maximum activity was observed in mature galls. The average values measured were 0.9±0.2, 1.9±0.5, 1.4±0.4, 1.4±0.4 mg m^{-1} dw in ungalled leaves, young, mature and old galls respectively (Table1). Peroxidases are a ubiquitous enzyme cluster, responsible to the catalytic reduction of peroxide and generate reactive oxygen species (ROS). Usually infestation by any arthropod will stimulate peroxidase activity in cell sap and enhance total soluble protein levels. In any such activity, peroxidases measured to indicate ROS production, a key stress indicator. The study also showed increased peroxidase activity in *T. nudiflora* galls, which is supported by the findings of Biswas *et al*. (2018).

Invertase activity

Increased invertase activity was highest in young galls.Average values are 3.7±0.5, 4.5±0.3, 4.3±0.2, 3.8±0.1 mg/min dw in ungalled leaves, young, mature, and old galls, respectively (Table1). Invertase is a sucrose-hydrolyzing enzyme found in plant tissues, serving as a physiological sink. Enhanced invertase activity was also reported by (Dsouza and Ravishankar, 2014) in psyllid galls of *Ficus glomerata* Roxb induced by *Pauropsylla depressa* Crawford, which is consistent with the present observations.

pH changes

The pH of ungalled leaves was observed to be slightly acidic, while, it was more acidic in galled tissues. The mean pH values observed were 6.052



Figs. (1) Adult - *T. fletcheri,* (2) Egg, (3) I instar, (4) V instar of *T. fletcheri,* (5) *T. nudiflora* plant, (6) isolated galls, (7) agglomerated mass of galls, (8) rosette galls (Photo courtesy: Dr. Om Datta)

Table 1. Metabolites in ungalled leaves and young, mature and old leaf galls of *Trewia nudiflora* induced by *Trioza fletcheri* on dry weight basis

Metabolites/ Plant parts	Ungalled	Young gall	Mature gall	Old gall
Total soluble sugars (mg g^{-1})	3.40±0.09	4.3±0.02	3.80±0.50	2.70±0.23
Total reducing sugar (mg g^{-1})	1.40±0.10	2.9±0.30	3.70±0.30	2.40±0.30
Total phenol (mg g^{-1})	0.63±0.03	1.9±0.47	1.03±0.04	0.83±0.03
Total protein (mg g^{-1})	1.90±0.23	3.7±0.36	2.90±0.35	2.60±0.34
Total free amino acids (mg g^{-1})	3.00±0.72	4.7±0.53	5.40±0.31	4.30±0.22
IAA-Oxidase	2.45±0.53	2.92±0.32	3.70±0.43	2.51±0.03
α-Amylase starch (mg/min)	2.40±0.30	3.2±0.20	3.60±0.40	2.90±0.40
Peroxidase (Δ A/g /min)	0.90±0.20	1.90±0.50	1.40±0.40	1.40±0.40
Invertase sucrose (mg/min)	3.70±0.50	4.50±0.30	4.30±0.20	3.80±0.10

±0.17, 5.916±0.10, 5.1±0.1, 5.58±0.09 and 5.95±0.12 in ungalled and gall-infested leaves, young, mature and old galls respectively. The pH of mature galls was recorded to be more acidic than that of ungalled leaves. Immature stages of *T. fletcheri* inject saliva into leaf tissues during feeding, which contains some chemicals that decrease the pH of galled tissues. The pH level of old gall tissues increases as the fifth instar immature comes out of the gall.

The study concludes that due to interaction between gall-inducing immature stages of *T. fletcheri* and plant tissue, certain biochemical and physiological changes occur in the leaves. Since the cells require a high amount of protein, the young and mature galled tissue show a major difference in protein concentration when compared to normal leaf tissue. When gall-inducing insects attack a plant, they inject elicitors that cause the plant to produce large numbers of various types of enzymes and metabolites as a defence mechanism against the biotic stress. Insects activate the plant's defence system, which starts several biochemical reactions and physiological processes that lead to the development of gall. Until the immature stages of gall-inducing insects live within the host, its metabolism gets altered to that extent that the galls show varying levels of metabolites. The study shows that feeding of immature stages of *T. fletcheri* leads to significant changes in metabolites such as total soluble sugars, reducing sugars, total protein, free amino acids, and increased activity of IAA-oxidase, α-amylase, peroxidase, and invertase in galled tissues of *T. nudiflora.*

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