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OXIDATIVE ENZYMES AND PHENOLS AS RELATED TO *SCHIMA KHASIANA* DYER NORMAL AND GALL TISSUES BOTH *IN VIVO* AND *IN VITRO*

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SUMMARY

The *in vivo* gall tissue of *S. khasiana* showed lesser activities of PRO and IAA–oxidase as compared to normal tissue. However, the PPO activity was higher in the former. In general, the gall tissue grown in the media containing different auxins, showed more PRO, PPO and IAA – oxidase activities as compared to normal. However, the normal tissue showed more PPO and IAA – oxidase activities in 2,4–D and IBA treatments, respectively. The gall tissues contained more total and o-dihydroxy phenols. By increasing the concentrations of different phenols in the assay mixture of IAA-oxidase, higher activities of this enzyme were recorded.

KEY WORDS

Schima khasiana, normal, gall, tissue culture, oxidative enzymes

ABBREVIATIONS

PRO, peroxidase; IAA, indole – 3 – acetic acid; PPO, polyphenol oxidase; 2,4–D, 2,4–dichlorophenoxyacetic acid; IBA, indole – 3 – butyric acid; MS, Murashige and Skoog; NAA, α-naphthaleneacetic acid

INTRODUCTION

The gall formation in plants following infection by different pathogens brings about a number of physiological and biochemical changes, both qualitative and quantitative at the level of growth hormones, oxidative enzymes and phenols (Kahl and Schell, 1982; Tandon and Arya, 1982; Kado, 1984; Joshi *et al.*, 1985). The higher levels of auxins in plant tumors (Tandon and Arya, 1980a; Weiler and Spanier, 1981; Kado, 1984) are reported to be responsible for their abnormal growth. However, the mechanism causing the hyperauxinic state still remains obscure.

Several differences have been reported in the activity of oxidative enzymes that are associated with tumour formation. Considerable indirect and some direct evidences suggest that the IAA-oxidase system is involved in the control of endogenous auxin levels and thus participates in the regulation of various physiological processes in both normal and tumour growth, such as cell growth and differentiation, and host-parasites interaction (ref. Sembdner *et al.*, 1980). In contrast, several investigators have reported that the differences in IAA-oxidase and PRO activities in normal and tumour tissues did not account for the increased amount of auxin (ref. Butcher, 1977). The presence of IAA-oxidase inhibitors and/or auxin protectors (phenolic compounds) has been observed in plant tumours by several workers (Tandon and Arya, 1980 a, b; Joshi and Tandon, 1989). Higher PPO activity and phenol contents have also been reported in crown gall (Wegen and Glase, 1981), mite-incited stem galls (Tandon and Arya, 1982) and leaf-roll galls (Joshi *et al.*, 1985). This paper describes the activities of PRO, IAA-oxidase and PPO and contents of phenolics in both *in vivo* and *in vitro* normal and gall tissues of *Schima khasiana*.

MATERIALS AND METHODS

Schima khasiana (family Ternstroemiaceae) are found at an elevation of 6,000 ft in Khasi Hills, Meghalaya. The insect, *Trioza* sp. (Homoptera),

attacks the young leaf just after the leaf flushing during May–June which results in gall formation.

Normal and gall leaf calli and *in vivo* tissues of the same were used as experimental material. Both normal and gall tissues were isolated and maintained on modified Murashige and Skoog's (1962) medium as described earlier (Rajee, 1988).

Tissue extract

200 mg of each of the above–mentioned tissues was homogenized in 5 ml of chilled 0.1 M potassium phosphate buffer at pH 6 and centrifuged at 5,000 g for 15 min at 0°C. The following assays were performed in both normal and gall tissues : (i) 1.11.1.7 peroxidase activity was determined according to the method as given in the Worthington Enzyme Manual (1972) with slight modification. The rate of decomposition of H_2O_2 by the enzyme with pyrogallol as hydrogen donor was determined spectrophotometrically by measuring the rate of colour development at 460 nm. The activity is expressed as change in absorbance/min/g acetone powder of tissue; (ii) 1.10.3.1. polyphenol oxidase was measured following Ponting and Joslyn (1948) and is expressed as change in absorbance/min/g acetone powder of tissue. The activity of IAA-oxidase was measured by the method of Tandon and Arya (1982). In the reaction mixture, first DCP was added to 0.1 M phosphate buffer pH 6 followed by $MnCl_2$, enzyme extract and then IAA. The total volume of the reaction mixture was kept at 5 ml having 0.2mM (final concentration) each of DCP, $MnCl_2$ and IAA. The reaction mixture was incubated at 37°C in a shaking water bath in the dark. After 1 hr, 2 ml of Salkowski reagent was added to each tube to terminate the reaction and following 1 hr wait, the absorbance of the mixture was measured at 530 nm. The amount of IAA destroyed was calculated from a standard curve for IAA. The enzyme activity is expressed as mg IAA destroyed/g acetone powder of tissue/hr.

Phenolics

Ethanol extract of lyophillized tissues was used to estimate the total and O-dihydroxyphenols using Folin Ciocalteu and Arnow's reagent, respectively (Mahadevan and Sridhar, 1982). Phenolics are presented as mg/g dry weight.

Effect of different phenolics on IAA-oxidase activity

Different phenolics like ferulic, caffeic, chlorogenic, protocatechuic, p-coumaric and shikimic acids and L-tyrosine and phloroglucinol in different

molarities (1.0 – 10mM) were added into the reaction mixture to study their influence on IAA – oxidase activity.

RESULTS

Oxidative enzymes

In vivo tissues

Of the two additives incorporated in the extraction buffer for the assay of PPO and PRO activities in *S. khasiana*, SDS was found better than PVP (Fig. 1). The optimum activities of PPO and PRO were recorded in extracts prepared in extraction medium containing 0.1 g each of SDS and PVP/g fresh wt. However, use of higher concentrations resulted in the decrease in the enzyme activities. The normal tissue of *S. khasiana* showed higher IAA oxidase and PRO activities as compared to gall tissues. However, a reverse picture was obtained for PPO activity. Both o-dihydroxy and total phenol contents were higher in gall tissues as compared to corresponding normal tissues (Table 1).

In vitro tissue

The *in vitro* grown gall tissue of *S. khasiana* exhibited higher PRO and PPO activities as compared to corresponding normal tissues in all treatments excepting 2,4–D for PPO activity (Table 2). There was a remarkable decline in the PRO activity of the normal tissues in case of 2,4–D treatment. Conversely, the PPO activity was much higher in the normal tissue.The gall tissues cultured in media containing different auxins showed higher IAA-oxidase activity as compared to normal, excepting IBA treatment, where a reverse picture was obtained. The *in vitro* gall tissues showed more o-dihydroxy and total phenol contents as compared to normal tissues subjected to auxin treatments except for control and 2,4–D treatments.

Effect of incorporation of different phenolics in assay mixture of IAA-oxidase

Addition of 1–10 mM of protocatechuic, ferulic, caffeic, chlorogenic, p–coumaric and shikimic acids and L-tyrosine and phloroglucinol in the assay mixture resulted in higher IAA–oxidase activities in normal and gall tissues of *S. khasiana* as compared to control excepting 1 mM of protocatechuic, ferulic, p-coumaric and shikimic acids and L-tyrosine (Fig. 2).

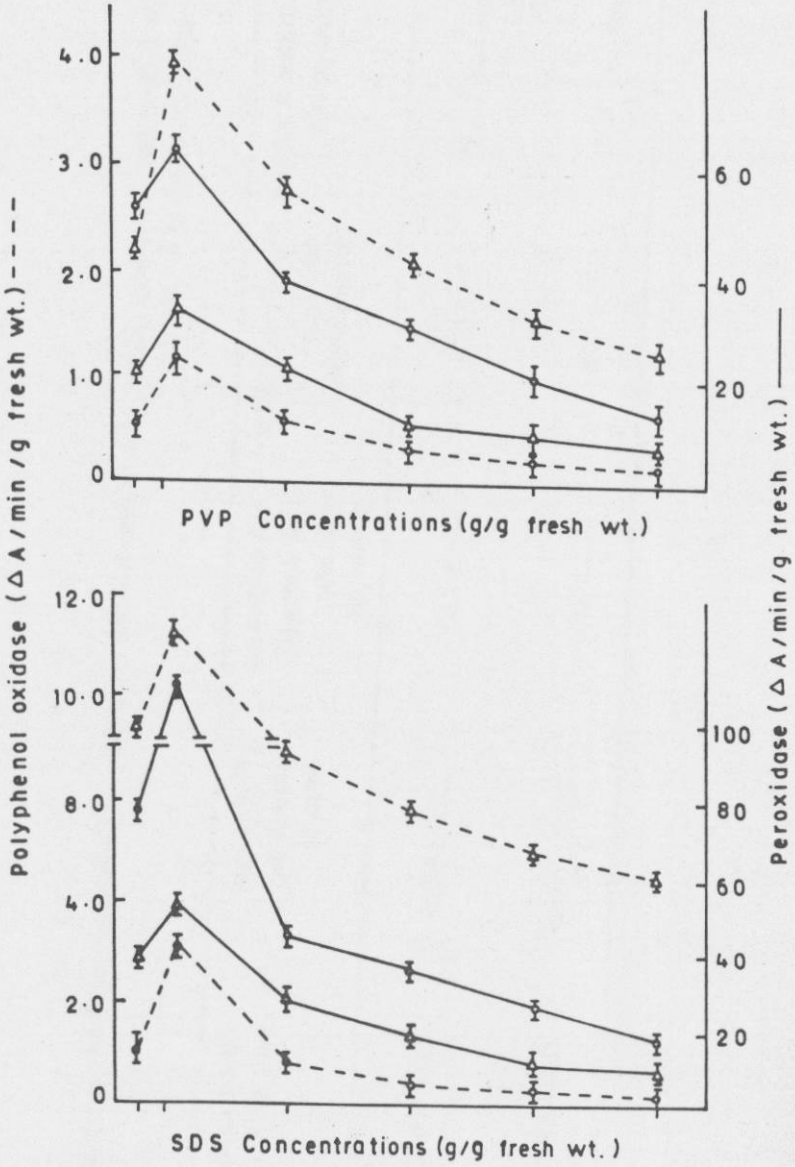

Fig. 1. Effect of incorporation of PVP and SDS in homogenizing media on polyphenol oxidase and peroxidase activities in *in vitro S. khasiana* normal (O) and gall (Δ) tissues.

Table 1. Peroxidase, polyphenol oxidase, IAA-oxidase activities and contents of O-dihydroxy and total phenols in *in vivo* normal and gall tissues of *S. khasiana*

Peroxidase Δ A/min/g acetone powder	Polyphenol oxidase ΔA/min/g acetone powder	IAA-oxidase mg IAA destroyed/ g acetone powder /hr	O-dihydroxy phenols mg/g fresh wt	Total phenols mg/g fresh wt
Nor- 14.6 ± 0.33 mal	0.25 ± 0.04	38.4 ± 1.10	0.039 ± 0.003	0.054 ± 0.004
Gall 1.4 ± 0.33	0.33 ± 0.06	26.2 ± 0.82	0.088 ± 0.004	0.144 ± 0.002

± S.E.

Table 2. Peroxidase, polyphenol oxidase, IAA-oxidase activities and contents of O-dihydroxy and total phenols in *in vitro* normal and gall tissues of *S. khasiana* grown in media containing different auxins (2 mg/l)

Treatment	Peroxidase ΔA/min/g acetone powder		Polyphenol oxidase Δ A/min/g acetone powder		IAA-oxidase mg IAA destroyed/g acetone powder/hr		O-dihydroxy phenols mg/g fresh wt		Total phenols mg/g fresh wt	
	Normal	Gall	Normal	Gall	Normal	Gall	Normal	Gall	Normal	Gall
NAA (Control)	86.60 ± 0.89	320.94 ± 3.02	3.79 ± 0.10	8.98 ± 0.05	13.2 ± 0.22	16.8 0.33	0.22 ± 0.03	0.67 ± 0.08	1.62 ± 0.08	1.35 ± 0.08
IBA	121.95 ± 1.00	179.77 ± 1.07	3.95 ± 0.13	1.12 ± 0.12	30.4 ± 0.23	19.1 ± 0.33	0.02 ± 0.001	1.22 ± 0.15	1.01 ± 0.08	6.86 ± 0.26
2,4–D	4.34 ± 0.14	250.02 ± 1.19	125.62 ± 8.13	6.65 ± 0.12	14.5 ± 0.22	29.0 ± 0.23	0.38 ± 0.02	0.47 ± 0.03	3.67 ± 0.33	0.94 ± 0.05
IAA	303.12 ± 4.13	422.22 ± 4.10	2.73 ± 0.43	38.88 ± 0.66	1.59 ± 0.11	5.0 ± 0.21	0.35 ± 0.03	0.40 ± 0.02	1.68 ± 0.08	2.43 ± 0.14

± S.E.

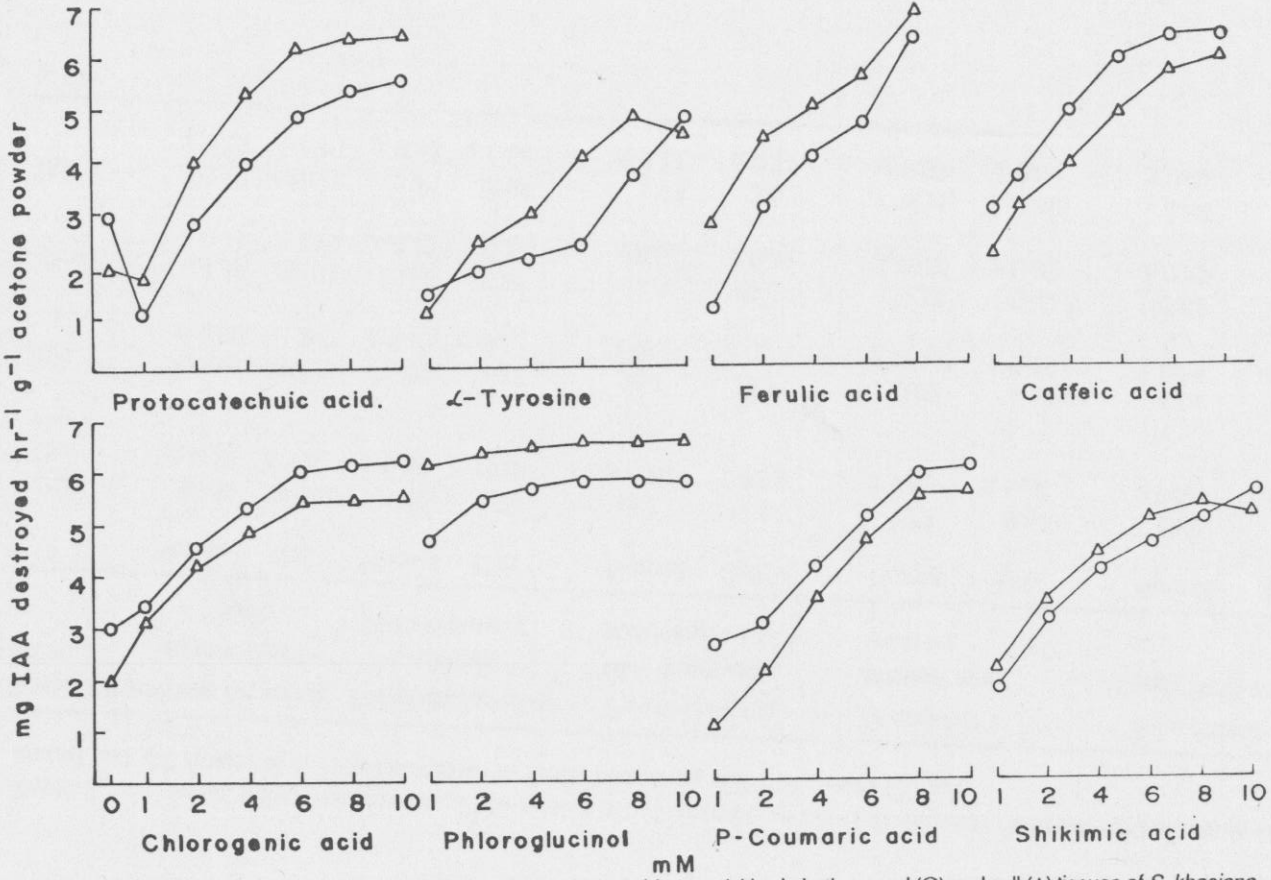

Fig. 2. Effect of different molarities of various phenolic acids on IAA–Oxidase activities in both normal (O) and gall (Δ) tissues of *S. khasiana*.

DISCUSSION

Schima gall tissue showed low IAA oxidase activity as compared to normal (Table 1). Decrease in the activity of IAA oxidase associated with mite-incited galls has been reported (Tandon and Arya, 1982; Joshi *et al.*, 1985). IAA catabolism in plant tumours has been a subject of extensive investigation and there are number of conflicting reports (ref. Butcher, 1973). The low IAA-oxidase activity and more total phenols in gall tissue of *Schima* may be responsible for its hyperauxinity. The involvement of phenols in the oxidation may result in inhibition or stimulation of plant growth metabolism. Several hypotheses have been proposed on this action of natural phenolic substances as factors which regulate the activity of IAA-oxidase, and also enable IAA synthesis from L-tryptophan (Kefeli and Kutacek, 1977).

Considerable evidence suggested that IAA-oxidase system is involved in the control of endogenous auxin levels and thus regulate various physiological processes as cell growth, differentiation and host-parasite interaction (ref. Sembdner *et al.*, 1980). It is generally accepted that there might occur a negative correlation between growth rate (auxin content) and IAA-oxidase activity of various organs or tissues (Zofia, 1984).

Plant enzymes are also greatly influenced by growth hormones in *in vitro* grown tissues (Barendse, 1983) and on the other hand, synthesis of phenolic compounds is influenced by auxin level in the medium. In contrast to *in vivo* tissues, the *in vitro* tissues showed more IAA-oxidase activity in different auxin treatments. A decrease in auxin content has been reported in both normal and gall calli grown in media containing NAA, IAA and DL-tryptophan (Tandon and Arya, 1980b). IAA-oxidase activity was more in the gall as compared to normal tissue of *S. khasiana* in the medium containing NAA, 2,4–D and IAA and vice versa in the medium containing IBA (Table 2). Bouillene and Gaspar (1970) have reported a high PRO and IAA–oxidase activity in *Impatiens* crown-gall tissue homogenates free from inhibitors. The interaction between IAA and various soluble phenols with oxidase preparations have long been studied. Machachova *et al.* (1975) found that the PRO preparation from *Triticum* shoots will oxidise ferulate more easily than p-coumarate. The enzyme is not able to directly oxidise IAA, even with exogenously supplied PRO, but required a phenolic co-factor such as p-coumarate. It was also suggested that PRO degradation of phenolics may be regulated by auxins in the intact plants, and further more, whether phenols or auxins are oxidised would depend on the concentration ratio of diphenols/monophenol/auxin.

The phenolic compounds are presumed to act indirectly through their effect on IAA-oxidase. Thus monophenols are inhibitory because they promote decarboxylation of IAA, whereas diphenols are growth promoters as they inhibit IAA-oxidation. Higher concentrations, however, are inhibitory. Though it is generally accepted that PRO is responsible for some IAA-oxidase activity, it is not clear whether a true oxidase exists distinct from PRO.

In numerous incompatible host-parasite combinations, PRO activity was several times higher than in compatible ones (Daly *et al.*, 1971). However, PRO activity was greater in compatible host-parasite combinations than in the incompatible ones (Wood and Barbara, 1971). Phytohormones are known to play a major role in growth and differentiation. The PRO functional to growth by its IAA oxidizing action and biosynthesis (Wheeler and King, 1968) and regulation of relationship of IAA synthesis in normal and tumorous tissue with PRO have been studied by several workers (Ahuja and Gupta, 1974; Bayer, 1982). Basu and Tuli (1972) suggested that the oxidative transformation of IAA to other biologically active compounds in plants may contribute to the IAA activity rather than to its inactivation.

Peroxidases are the major components in the IAA-oxidase system in plant. The rapid decline in the PRO activity from high to low level in the gall tissue might result in sparing the auxin from being oxidised. This sparing action of IAA-oxidation is provided by the low or high polymers of O-dihydroxyphenols. Interaction of IAA-oxidation with phenolics such as ferulic, hydroxycinnamic acid, and scopoletin and to the complexity of the system (Sirois and Miller, 1972; Gelinas, 1973). PRO relationship to polyphenol and IAA-oxidase have been suggested (Gove and Hoyle, 1975). In general, PRO catalyses four type of reactions (i) peroxidative (ii) oxidative (iii) catalytic and (iv) hydroxylation (Vamos-Vigyazo, 1981). The gall tissues showed higher PRO activity as compared to normal, when grown in the medium containing NAA, IBA, 2,4–D and IAA (Table 2). In general, maximum activity was observed in the medium containing NAA followed by IAA and 2, 4–D, whereas with IBA treatment the gall tissue showed the least PRO activity. It is shown that the oxidation of IAA takes place in several steps in which different intermediates rather than the native form are believed to be responsible for the breakdown of certain phenolic inhibitors (Gelinas, 1973).

Higher PPO activity was observed in gall tissues as compared to normal (Table 1). The increase in activity in the host tissues especially at

and around the infection sites is a response which is characteristic to a large number of plant diseases. The phenolase activity is accompanied with increase in phenolic concentration, which plays a role in toxicity of pathogen (Kosuge, 1959). Increased O-dihydroxy and total phenol concentrations in gall tissue as compared to normal (Table 1) could be due to higher activity of PPO in gall tissues.

It was thought that PPO enzyme may participate in redox reaction within the plant cells. However, neither this nor localization of this enzyme has been demonstrated definitely. IAA is oxidized probably by the products of oxidation of catechol, i.e., by O-quinone. However, Pelet and Gaspar (1968) suggested only a temporary formation of complex between IAA and the oxidized phenols.

The increased PPO activity and phenolic contents has been reported in crown-gall (Wegen and Glase, 1981), mite-incited stem galls (Tandon and Arya, 1982) and leaf roll galls (Joshi and Tandon, 1984). The gall tissues of *S. khasiana* showed higher PPO activity than normal in the medium containing NAA, IBA and IAA. However, exceptionally high PPO activity was recorded in the normal tissues grown in the medium containing 2, 4–D. *Zizyphus* gall tissues contained less activity of PPO as compared to the normal tissues under the influence of NAA, IAA, 2, 4–D (Tandon and Arya, 1982). Interestingly, PPO activity decreased, whereas IAA-oxidase and PRO activities increased in the gall tissues of *Schima* in the medium containing 2, 4–D (Table 2). This supported the earlier findings on *Zizyphus* that the incorporation of growth regulators like 2,4–D in the culture medium decreased the auxin content in gall tissue (Tandon and Arya, 1980ab). Both *in vivo* and *in vitro* cultures of gall tissues in the medium containing NAA, IBA or IAA showed more PPO activity. Thus it may be suggested that gall formation is followed with production of factor(s) essential for higher PPO activity by the growth regulators that could trigger switching off and on of IAA–oxidase to regulate auxin contents.

Phenolic compounds are widely distributed and spread in nature. These compounds play a great role in normal and abnormal plant growths (Kefeli and Kutacek, 1977; Rosenthal, 1986) by their effect on enzymatic oxidation reaction. Many natural phenols interfered with indole biosynthesis (Kefeli and Kutacek, 1977) and oxidation of IAA *in vitro*. The lowest oxidation products of phenolic substances – the quinones, are most toxic and are highly oxidized and on the other hand polymerized products of polyphenols are considered less toxic or non-toxic.

The action of phenolic compounds on plant growth is frequently attributed to their interaction with IAA-oxidase, regulating IAA levels *in vivo* (ref. Letham, 1978). Sinapic and ferulic acids are known to be inhibitors of IAA-oxidase activity, thereby showing an auxin sparing effect. A similar observation was recorded in both normal and gall calli of *Schima* with the addition of ferulic acid in the medium. However, the results obtained indicated that the phenolic compounds tested show differential response to IAA–oxidase inhibition of which callus growth may be taken as an index of oxidation products.

From the results obtained it is clearly indicated that lower concentrations of phenols showed better effects on IAA–oxidase activity. Caffeic acid, chlorogenic acid and phloroglucinol were less inhibitory as compared to protocatechuic, ferulic, p-coumaric, shikimic acids and tyrosine. Higher concentrations of most phenolics inhibit growth irrespective of hydroxylation pattern. From the findings discussed above, it is evident that there existed an association of oxidative enzymes and phenols in the abnormal growth of *S. khasiana* gall tissues.

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