

Effects of leachates of *Casuarina equisetifolia* on photosynthesis and antioxidant enzymes of *Vatica mangachapoi* seedlings

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ABSTRACT

To explore the possibility of developing mixed forest of *Casuarina equisetifolia* L. and *Vatica mangachapoi* Blanco. we studied the effects of *C. equisetifolia* allelochemicals from the roots, rhizosphere soil and litter leachates on the photosynthesis, chlorophyll fluorescence parameters and the antioxidant activities of *V. mangachapoi* seedlings in laboratory trials. The leachates reduced the photosynthetic rate (Pmax), light compensation point (LCP), the maximum photochemical efficiency of PSII (Fv/Fm), the potential activity of PSII (Fv/Fo), apparent electron transfer efficiency (ETR) and the actual photochemical efficiency (Y) of *V. mangachapoi* seedlings. However, the light saturation point (LSP) and the initial fluorescence (Fo) were increased. The activity of superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR) and the content of MDA increased but the activity of peroxidase (POD) was reduced by the leachates treatment and habitat changes.

Key words: Allelochemicals, antioxidant enzyme system, *Casuarina equisetifolia*, leachates, photosynthesis characteristics, *Vatica mangachapoi*

INTRODUCTION

Since the 1950's, *Casuarina equisetifolia* is widely planted in south east coast of China as wind break and soil conservation forest. Now this forest is decaying and has difficulty in replenishing itself due to its allelopathic effects on the surrounding organisms. It also suffers from severe diseases and pest manifestation, which decreased its ability to protect the coastline. Planting of forests with multiple species, especially the native species, has been proposed as an alternative to improve the soil conservation capability of these forests (35).

Until now, the researches on *C. equisetifolia* have been done on the genetic diversity (15,23,36) and the growth under different habitats (24,25,31). However, the study of its leachates was done only by Deng's (6). Five allelochemicals (kaempferol-3- α -rhamnoside, quercetin-3- α -araboside, luteolin-3', 4'-dimethoxy-7- β -rhamnoside, kaempferol-3- β -dirhamnoside and quercetin-3- β -glucoside) from *C. equisetifolia* branchlet were isolated and identified by HPLC and three of them inhibited the growth of its seedlings. The analyses of allelopathy of different clone and different density of

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C. equisetifolia and the influence of associated tree species and fertilization on the *C. equisetifolia* showed that the main reason of the re-planting problem was due to the allelochemicals, which inhibited the self growth i.e. autotoxicity (19,20). Little research had been done on the effects of *C. equisetifolia* allelochemicals on associated tree species.

Plant releases allelochemicals in to its surrounding environment and mostly in soil by leaching, volatilization, litter, and residue decomposition. A better understanding of effects of allelochemicals in *Casuarina* soil environment (such as roots, litter, and rhizosphere) on the surrounding plants is important. In previous studies, we studied the effects of the leachates of *C. equisetifolia* branchlets on seed germination and the response of photosynthetic characteristics of *Vatica mangachapoi* (17). Furthermore we isolated and identified the leachates of roots, soil and litter of *C. equisetifolia*, and analyzed effects on the photosynthesis, chlorophyll fluorescence parameters, the activities antioxidase system and comparative proteomics under different leachates and habitats. In this experiment, we studied the effects of leachates of *C. equisetifolia* roots, rhizosphere soil and litter on the *V. mangachapoi* seedlings under different habitats.

MATERIALS AND METHODS

Experimental Design

The litter, roots and soil of *Casuarina equisetifolia* were collected in the forest on the coast of Guilinyang town, Haikou (110° 29'E, 20° 1' N); air dried in shade, then soaked in distilled water for 24 h (sample 1kg : water 4L). The leachates were collected by filtering the mixture through four sheets of filter paper. The leachates were then diluted with distilled water to get concentrations of 0.125g/ml. Distilled water was used as control.

Seedlings at 2 true leaf stage of *V. mangachapoi* were collected from the coast of Shimei Wan, Hainan Island, China (110° 16'E, 18° 40' N) in July 2009 and 2010. They were planted in plastic pots (25 cm dia and depth) and each pot was irrigated with 250 mL *C. equisetifolia* leachates of litter, roots and soil once every 2 days and distilled water was used as control. Another set of *V. mangachapoi* seedlings at the same stage were planted in a *C. equisetifolia* forest as the immigrant area, and watered in the first month to ensure the survival of seedlings. Meanwhile a separate set of seedlings at the same stage were planted in a *V. mangachapoi* forest to mark as control (native). The soil parameters of the immigrant area and native area are given in Table 1. After 3 months, the following procedures were conducted. There were 3 replicates.

Table 1. Soil chemical properties in different habitats

Area	pH	OM(g kg ⁻¹)	TN(g kg ⁻¹)	TP(g kg ⁻¹)	TK(g kg ⁻¹)
Native areas	5.14	263.02	0.66	0.22	12.21
Immigrant areas	4.68	446.94	0.24	0.57	10.28

OM: Organic matter, TN: Total N, TP: Total P, TK: Total K

Photosynthesis measurements

V. mangachapoi seedlings were analyzed with an LI-6400 portable photosynthesis system. Net photosynthesis rate (Pn), stomatal conductance (Cond), intercellular

CO₂ concentration (C_i), and transpiration rate (Tr) were measured, a photosynthesis-photo and photosynthesis-CO₂ curve were generated. The detail methods can be found in previous research (17).

Chlorophyll fluorescence measurements

V. mangachapoi seedlings were analyzed with Os5p multi-mode chlorophyll fluorometer: Fo (Dark adapted initial fluorescence value), Fm (Maximal fluorescence), and Yield (Effective quantum yield) were measured, Fv (Variable fluorescence), Fv/Fm (Maximum quantum yield-Photochemical efficiency of PSII), Fv/Fo (PSII potential activity), and ETR (Electron Transport Rate) were generated.

Activity of Protective Enzymes and MDA

Superoxide dismutase (SOD) activity was determined based on its capacity to inhibit reduction of nitroblue tetrazolium (NBT) (9). Catalase (CAT) and glutathione reductase (GR) activity was determined with Jiang's method (13), and peroxidase (POD) was determined with Cakmak's and Kraus' method (5,16). The content of malondialdehyde (MDA) was determined according to the methods of Buege *et al.* (4).

Statistical analysis

All analyses were done in 3 replicates. Statistical significance was determined by SPSS (16.0) and LSD (least significant difference method) tests. Differences were considered statistically significant when $P < 0.05$.

RESULTS AND DISCUSSION

PHOTOSYNTHESIS

Photosynthetic active radiation

The net photosynthetic rate (P_n) increased with the increasing photosynthetic active radiation (PAR). The P_n of control groups were higher than other treatment groups. The P_n in native areas was higher than in immigrant areas. The results showed that *C. equisetifolia* leachates reduced the P_n of seedlings (Figs 1 and 2)

The variance among the different treatments is also displayed through the different parameters in the photosynthesis curve. The LSP, LCP, P_nmax and AQY were calculated from the Farquhar model and were organized in linear regression. The light saturation point (LSP) was 9.14% (litter extract), 12.57% (root extract), 11.43% (soil extract) and was significantly higher than control. There were no significant differences among the treatment groups. LSP in immigrate areas were significantly higher than in native areas (120.59%) (Figure 3).

There were significant differences ($P < 0.05$) between the treatment groups and controls, and also between the immigrant areas and the native areas. Thus a change in habitat and treatments with different leachates increased the LSP. The light compensation point (LCP) were 21.59% (litter extract), 21.67% (root extract), 57.26% (soil extract) and were lowered than control. However, there were no differences between the immigrate areas and native areas (Fig. 3).

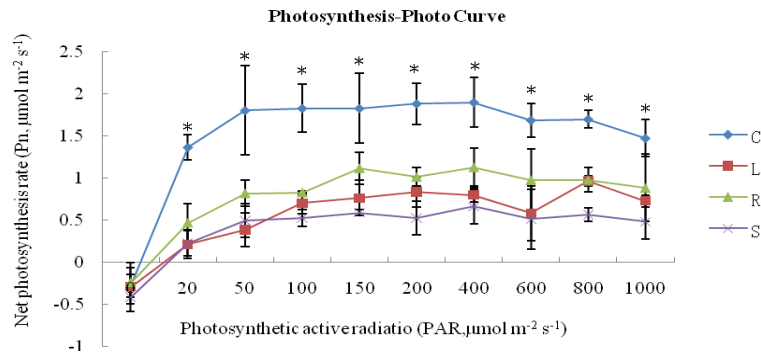


Figure 1. Effects of various leachates of *C. Equisetifolia* ($p > 0.05$) on photosynthesis-curve of *V. mangachapoi*. C: Control, L: Litter leachates, R: Root leachates, S: Soil leachates.

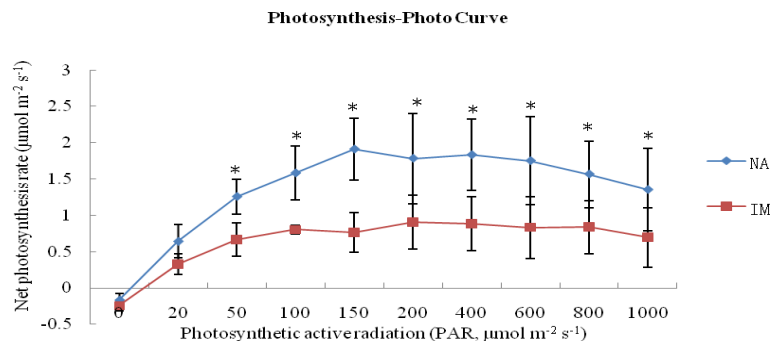


Figure 2. Effects of native and immigrant areas ($p > 0.05$) on photosynthesis-photo curve of *V. mangachapoi* seedling. NA: Native areas, IM: Immigrant areas.

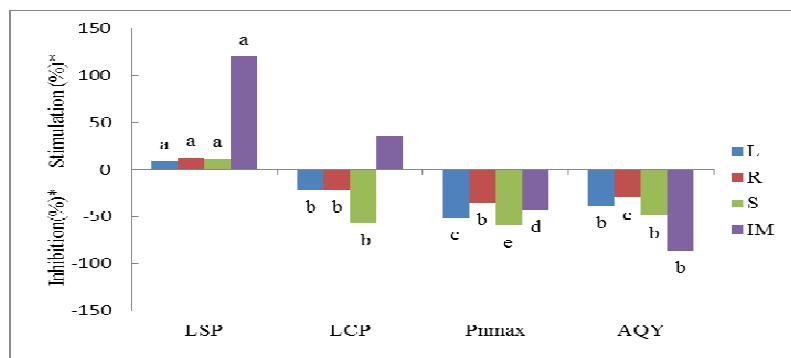


Figure 3. Effects of various leachates of *C. Equisetifolia* and in immigrant areas on photoresponse parameters of *Vatica mangachapoi*. * : % Inhibition/ Stimulation over control. L: Litter leachates, R: Root leachates, S: Soil leachates, IM: Immigrant areas, LSP: Light saturation point, LCP: Light compensation point, Pnmax: Maximal RuBP regeneration rate, AQY: Apparent quantum yield. The different letter indicate significant differences at the 0.05 level.

The different leachates treatment significantly inhibited the Maximal RuBP regeneration rate (Pnmax) and were 51.25% (litter extract), 35% (root extract), 59.17% (soil extract), 42.54% (in immigrate areas). The Apparent quantum yield (AQY) were 38.46% (litter extract), 29.81% (root extract), 49.04% (soil extract), 86.22% (immigrate areas) respectively. The data of Maximal RuBP regeneration rate (Pnmax) and Apparent quantum yield (AQY) showed that a change in habitat and treatments with different leachates significantly decreased the Pnmax and AQY (Fig. 3).

The response of photosynthesis to PAR showed that a change in habitat and treatment with the different leachates of *C. equisetifolia* reduced the Pn and LCP of seedlings, but increased the LSP. Similar results reported in other plants (7,18,26,33,34). A higher LSP means increase in the ability of plants to use strong light and a lower LCP means that seedling can use weak light (41), so higher LSP and lower LCP means the increasing ability of light use. That means a change in habitat and treatment with different leachates increases the ability of light use. Our study, speculated that decrease in Pn is not caused by light use.

Pn max and AQY expresses the rate of electron transport and activity of photophosphorylation, i.e photosynthetic capacity. The simultaneous decrease in Ps and AQY is prominent characteristic of photoinhibition when photosynthetic organs were damaged (33). Our results of Maximal RuBP regeneration rate (Pnmax) and Apparent quantum yield (AQY) showed that a change in the habitat and treatment with different leachates significantly decreased the Pn max and AQY (Table 2). It means that a change in habitat and treatment with different leachates affected the photosynthesis.

CO₂ concentration

The photosynthetic response to CO₂ concentration was noticed when photosynthetic active radiation (PAR) was set to 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Figs 4 and 5). With the increase in CO₂ concentrations, the Pn of treatment groups increased proportionally. At low levels of CO₂ concentrations, the Pn increased slowly. When CO₂ concentration was > 200 $\mu\text{mol mol}^{-1}$, Pn increased rapidly. The results also indicated that the Pn of controls and subjects in native areas were always higher than treatment groups.

The CSP, CCP, Pnmax and CE parameters were calculated from the Farquhar model and were organized in linear regression. The CO₂ saturation point (CSP) were slightly higher [15.89% (litter extract), 1.91% (root extract), 15.83% (soil extract), 5.26% (immigrate areas)] than control. The CO₂ compensation point (CCP) of treatments were 91.61% (litter extract), 104.6% (root extract), 125.5% (soil extract), 84.95% (immigrate areas) and were higher than control and native areas. Maximal RuBP regeneration rate (Pnmax), carboxylation efficiency (CE) of all treatments were lower than control (Fig. 6). The results showed that a change in habitat and treatments with different leachates significantly inhibited the Pnmax and CE (Fig. 6).

The lower CO₂ saturation point (CSP) and CO₂ compensation point (CCP) means stronger fixation of CO₂ at low concentrations. CE is used as an index of Rubisco, because there is a positive correlation between CE and the activity of Rubisco (18,28). Our results showed that leachates increased the CSP and CCP. However the treatment and a change in habitat decreased the CE. It implied that concentration of environmental CO₂, intercellular CO₂ and the activity of Rubisco are the limiting factors for the photosynthesis when the habitat was changed and seedlings of *V. mangachapoi* were treated with different leachates.

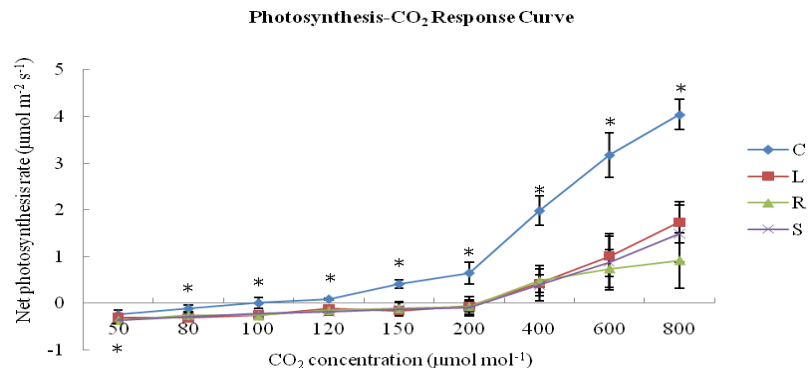


Figure 4. Effects of CO₂ and leachates of *C. equisetifolia* ($p > 0.05$) on photosynthesis rate of *V. mangachapoi* seedlings. C: Control, L:Litter leachates, R:Root leachates, S:Soil leachates.

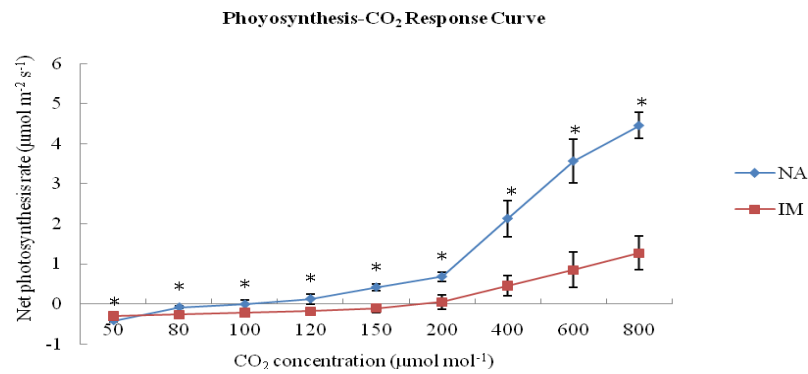


Figure 5. Effects of CO₂ in native and immigrant area ($p > 0.05$) on photosynthetic rate of *V. mangachapoi* seedlings. NA: Native areas, IM: Immigrant areas

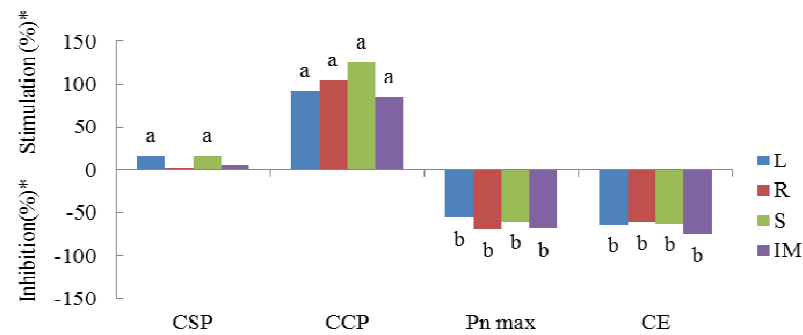


Figure 6. Effects of various leachates of *C. Equisetifolia* and in immigrant areas on CO₂ response parameters of *Vatica mangachapoi*. * : % Inhibition/ Stimulation over control.L: Litter leachates, R: Root leachates, S: Soil leachates, IM: Immigrant areas. CSP: CO₂ saturation point, CCP: CO₂ compensation point, Pnmax: Maximal RuBP regeneration rate, CE: Carboxylation efficiency. The different letter indicate significant differences at the 0.05 level.

Chlorophyll fluorescence

F_o (dark adapted initial fluorescence) were 19.61% (litter extract), 14.22% (root extract), 15.69% (soil extract), which were higher than control. There were significant differences among the treatments, but results were similar in immigrant areas (10.71%)(Fig. 7).

The value of F_v/F_m and F_v/F_o were: soil extract (-7.64%, -28.52%) were most inhibitory, root leachate (-3.76%, -16.13%) and litter leachate(-1.88%, -8.37%). These parameters were decreased than control and showed significant differences between them. The results were similar in immigrant areas (-5.35%, -22.16%) (Fig. 7).

Actual photochemical efficiency of PSII in light (Yield) and electron transport rate (ETR) validated these results. Yield and ETR of all treatments declined [-1.72% and -9.09% (litter leachate), -3.97% and -18.18% (root leachate), -2.78% and -4.55% (soil leachate)] but significantly differed among them (Fig. 7). The data in NA and IM had similar results. The decrease in Yield and ETR of all treatments and individuals in the immigrant areas blocked the formation of assimilate power (NADPH, ATP) and influenced the CO₂ fixation.

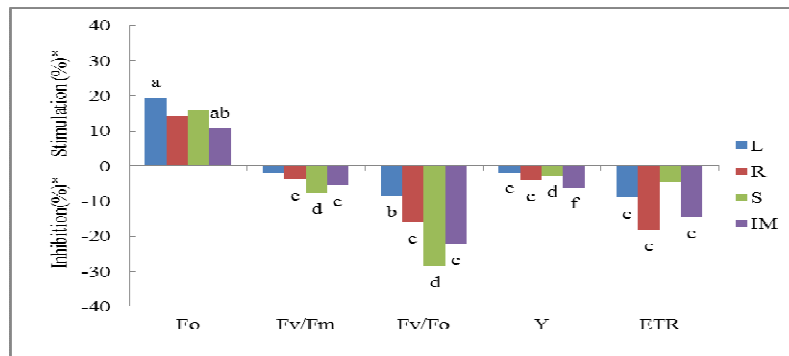


Figure 7. Effects of various leachates of *C. Equisetifolia* and in immigrant areas on chlorophyll fluorescence parameters of *Vatica mangachapoi*. * : % Inhibition/ Stimulation over control. L: Litter leachates, R: Root leachates, S: Soil leachates, IM: Immigrant areas, F_o: Dark adapted initial fluorescence value, F_v/F_m: Maximum quantum yield-Photochemical efficiency of PSII, F_v/F_o: PSII potential activity, Y: Effective quantum yield, ETR: Electron Transport Rate. The different letter indicate significant differences at the 0.05 level.

F_o, F_m, Yield and ETR indexes of affected photosynthesis ability, especially photosynthetic electronic transport rate and photochemical efficiency of PSII (2,22). An increase of F_o means more energy was used in heat dissipation, but less energy was used to move the electron transport chain of PSII (7,10,40). F_v/F_o represents the potential photochemical efficiency of PSII (7). F_v/F_m is an estimate of the maximum portion of absorbed quanta used in PSII reaction centres. A higher F_v/F_m means that photosynthetic organs can convert captured light into biochemical energy, so usually it is an index of photoinhibition of PSII. The decline of F_v/F_o and F_v/F_m are also correlated positively with the stress degree (29,39). Our results showed that F_v/F_o and F_v/F_m decreased inversely in different treatments, than control. Y and ETR also decreased, which means

that treatments with different leachates and habitat affected the PSII. Plants can form various energy dissipation mechanisms, reduce the damage to photosynthetic apparatus and effectively protects the reaction centre of PSII against the damage from excessive light energy. Our results showed that F_o increased under different treatments than control. It implies that the seedlings leaves lose the excess energy through heat dissipation to protect reaction centre of PSII from excessive stress of different leachates and change of habit. Similar results were found in studies of Han and Yang (10,34).

C. *EQUISETIFOLIA* LEACHATES

Antioxidant enzymes

Cell membrane peroxidation: MDA is one of the final products of peroxidation of unsaturated fatty acids in phospholipids and is responsible for cell membrane damage (9,13,14). MDA contents of treatments were 141.23% (litter extract), 93.81% (root extract), 105.15% (soil extract), 31.32% (immigrate areas) and were higher than control (Fig. 8). The results showed that allelochemicals stress caused MDA to accumulate the metabolites of active oxygen and free radicals to become unbalanced. The peroxidation of cell membrane injured the structure and function of cell membranes. However, there was no difference between the individuals in immigrant areas and in native areas (Fig. 8).

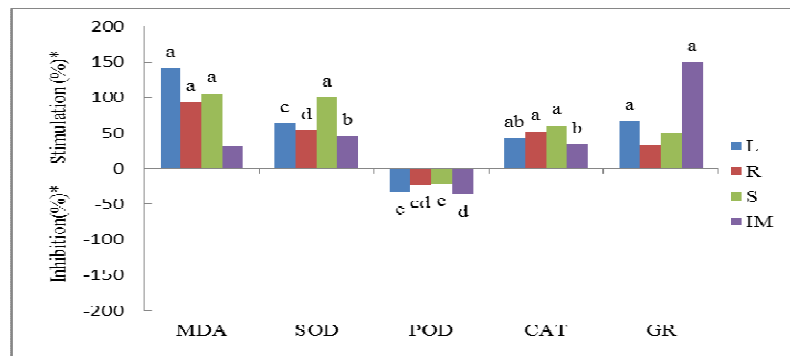


Figure 8. Effects of various leachates of *C. Equisetifolia* and in immigrant area on activity of antioxidant enzyme system of *Vatica mangachapoi*. * : % Inhibition/ Stimulation over control. L: Litter leachates, R: Root leachates, S: Soil leachates, IM: Immigrant areas. MDA: malondialdehyde, SOD: superoxide dismutase, POD: peroxidase, CAT: Catalase, GR: glutathione reductase. The different letter indicate significant differences at the 0.05 level.

Protective enzymes

Besides injuring the cells, the increase in active oxygen may also act as defence chemical signal to startup antioxidant enzyme systems by inducing many reactions of other signals. SOD, POD, CAT and GR are important enzymes for clearing the free radicals and maintaining the membrane system (9,13,14). The activity of SOD, CAT and GR of treatment groups were higher than control. The activity of SOD, CAT and GR of all treatments showed decrease of 63.89%, 42.91% and 66.67% (litter leachate), 54.04%,

51.99% and 33.25% (root leachate), 100.09%, 60.87% and 49.92% (soil leachate), 46.14%, 33.75% and 149.88% (immigrate areas). The SOD activity differed in treatments, but the activity of CAT and GR were similar. The activity of POD declined [33.3% (litter extract), 24.08% (root extract), 21.0% (soil extract), 36.04% (immigrate areas)] and was different than other enzymes. The POD activity in treatment groups was lower than control (Fig. 8).

That means the POD was injured and reduced the clearing of H_2O_2 in cells. The other reason may be that there were too many H_2O_2 molecules under the allelochemical stress and in immigrant areas to be cleared by POD, decreasing the activity. Various environmental stresses leads to excessive production of ROS (Reactive oxygen species) causing progressive oxidative damage and ultimately cell death. Excessive ROS are detrimental because they cause damage of membranes, proteins, chlorophyll, and nucleic acid (11,21,38). To reduce this oxidative damage, plants use complex defence mechanisms, including non-enzymatic antioxidants and enzymatic antioxidants. Antioxidant enzymes play major role in protection of plant tissues under stressful conditions, viz., super-oxide dismutase (SOD), catalase (CAT), peroxidase (POD) and glutathione reductase (GR) (11).

In our study, MDA contents of treatment groups were higher than control. The results imply that the allelochemical stress induced ROS generation and cell membrane peroxidation, injured the structure and function of cell membrane system. Similar results were reported for allelopathy of *Lantana camara* (32).

SOD play a crucial role in functioning of ROS homeostasis regulation (30). It catalyzes O_2^- into H_2O_2 and O_2 (27), the H_2O_2 and O_2 can be cleaned by POD and CAT. It can maintain lower ROS by cooperating of SOD, CAT and POD, reduce the cell damage, as well as POD is a functional enzyme of plant respiration (3), so its activity is related to the respiration reaction. GR reduces GSSG into GSH, which is an important antioxidant of non-enzymatic reaction, and NADPH from photosynthesis as electron doner (1), so GR is antioxidant enzyme, as well as related to plant photosynthesis. Our results showed that the activity of SOD, CAT and GR increased under different treatments and in immigrant areas, that implies that seedlings of *V. mangachapoi* can induce SOD, CAT and GR to clear the ROS and reduce the damage to cells caused by the allelochemical stress. Some studies imply that the increase of MDA content is physiological response that can result in peroxidation of membrane lipids with loss of membrane integrity (8,12,32). However, in our data the activity of POD was different from other enzymes, namely the activity of POD of treatment groups and in immigrant areas was lower than controls. By the above studies can be seen, the change of habitat and different leachates *C. equisetifolia* have made a great impact on the physiology of the *V. mangachapoi* seedlings.

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